EFFECTS OF AGRICULTURAL LAND USE ON TREE SWALLOW (*TACHYCINETA BICOLOR*) REPRODUCTION, BODY CONDITION AND DIET

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By

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ABSTRACT

Agricultural practices have intensified over the last 50 years, increasing crop production and altering the Canadian Prairie landscape by removing non-cropped habitats and wetlands. The productivity, trophic structure and diversity have changed through increased agrochemical inputs and reductions in yearly rotation and diversification of crop types. Most intensive agricultural practices have negative effects on invertebrate communities that can indirectly affect higher trophic organisms, such as birds. Many populations of aerial insectivorous bird species have been experiencing rapid declines in the last 30–40 years. Dependency on high abundances of aerial insects for reproduction and survival is a common link among all species of this guild. My thesis examined aerial insect abundance as a potential link between agricultural land use and the reproductive ecology, nestling body condition, and diet of an aerial insectivore species, the tree swallow (*Tachycineta bicolor*). My broad goal was to determine whether agriculture has deleterious effects on timing of breeding, reproductive investment and success, and nestling quality, as mediated by food supply and differences in diet.

Aerial insect abundance and biomass estimates obtained from passive insect traps which capture primarily aquatic dipterans were similar between agricultural and reference sites during all stages of breeding. However, estimates derived from sweep-net sampling in terrestrial habitats in 2013 indicated higher abundances of aquatic and terrestrial Diptera at a reference site relative to agricultural sites. Multiple measures of tree swallow productivity were not related to agriculture land use but nestling body condition was significantly lower on agricultural sites.

Using stable isotope analysis (δ^{13}C and δ^{15}N), I found site and age specific differences in swallow diets and isotopic niche widths but variation was not consistently related to agricultural land use. Aquatic insect prey (Diptera and Odonata) made up the majority of the diet of swallows

but nestlings had a larger proportion of terrestrial Diptera which resulted in larger isotopic niche widths compared to adults. The assimilated isotopic diet of nestling and adult swallows were not strong predictors of body size, mass or condition, suggesting that site differences in the diet do not appreciably affect condition.

Nestlings raised on agricultural sites had lower body condition that was not directly linked to their diet alone. This suggests other unmeasured factors related to agricultural land use may affect nestling tree swallows. This study tested responses in an aerial insectivore species to land use and potential shifts in the insect community, which may provide important information for conservation and management decisions for many species within the aerial insectivore guild.

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CHAPTER 1. GENERAL INTRODUCTION: AGRICULTURAL LAND USE PRACTICES AND AVIAN REPRODUCTION AND DIET

With the onset of the "Green Revolution" in the 1960s, farming techniques were modified to favour intensive agricultural practices and increase crop yield for food production (Gleaser 2011). Consequently, the development of genetically modified crops and advances in mechanical technology transformed agricultural practices which increased efficiency of crop production, crop yields and intensity of agricultural production without major changes in the amount of land converted to agriculture (Tilman et al. 2002). Intensification includes changes in agricultural practices that create extensive monocultures, reduce crop rotation, increase reliance on chemical inputs, modify timing and practice of mechanized seeding and harvesting, and remove or degrade non-farmed habitats such as wetlands and hedgerows (Matson et al. 1997, Stoate et al. 2001, Tscharntke et al. 2005). This revolution and further development in later years resulted in a dramatic shift from smaller, "mixed" farms to larger farms dominated by crop monocultures throughout Europe and North America.

Current trends of agricultural intensification in Canada show a 38% increase from 1986 to 2011 in the area of cropland and summer fallow per farm which is due to larger proportions of cropland to total farmland area in Canada and lower number of farms (Census of Agriculture 2011). Extensive expanses of land such as summer fallow and non-cropped land (i.e., hedgerows, field margins, wetlands) declined during this period to accommodate more "conservation tillage" practices and development of continuous cropping (Agardy et al. 2008, OECD 2008). Wetlands within Prairie Canada have been reduced by 40–70% (Rubec 1994, Whigham 1999, Dahl 2000) and wetland conversion to agricultural land through drainage and ploughing accounts for 85% of these losses (Agardy et al. 2008). Favoured agricultural practices may not only affect landscape

heterogeneity but reduce the productivity of intact land features such as wetlands, field margins, and hedgerows. As such, negative effects from the removal of semi-natural habitats and alteration of land use on lower trophic-level organisms, such as invertebrates (Meek et al. 2002, Savage et al. 2011, Fenoy and Casas 2015) could have subsequent impacts on higher trophic levels, including farmland birds (Wilson et al. 1999, Shortall et al. 2009).

1.1 RELATIONSHIP WITH DECLINING AERIAL INSECTIVORES

Abundances of many species of aerial insectivorous birds have declined in the past 30–40 years. Within Canada, this trend is apparent in 23 of 27 species of aerial insectivores (Calvert 2012). Hypotheses proposed to explain these population declines include habitat degradation and loss, climate change, exposure to contaminants and reductions in their main food source, aerial insects. Of these hypotheses, declines in aerial insect abundances represent a potential threat to all aerial insectivore populations as they are all reliant on high abundances of insects, often of aquatic origin, for successful reproduction and survival (Nebel et al. 2010). The relationship between insects and birds is complicated by impacts from numerous stressors on aerial insect abundance which in turn can indirectly influence populations of aerial insectivores. Thus, it is important to understand factors affecting aerial insects and in turn determine how these influence higher trophic level consumers, such as aerial insectivorous birds.

Many studies have reported lower insect abundance and diversity in areas under intensive agricultural practices (O'Leaske et al. 1997, Wilson et al. 1999, Vickery et al. 2001). Expansion of cropland area at the expense of semi-natural habitats such as wetlands and grassy field-margins negatively affects insect availability and species richness for farmland bird populations (Duelli et al. 1999, Wilson et al. 1999, Di Giulio et al. 2001, Grüebler et al. 2008). Changes in

the insect community are apparent across levels of increasing agricultural intensity, as Evans et al. (2007) reported high aerial insect abundances in pasture, followed by lower abundances in hay silage and then in cereal crops. Combined effects of pesticide applications with landscape changes through the removal of natural, grassy habitats for monoculture crops, control pest insects but also negatively affects non-target insect species such as aerial insects that are preferentially consumed by aerial insectivorous birds (Kragen et al. 2011). Insecticide application negatively affected species richness of Chironomidae (Diptera) near water bodies (Delettre and Morvan 2000). As well, abundances of Chironomidae declined by two orders of magnitude in insecticide-treated ponds relative to untreated ponds (Morrill and Neal 1990).

Agricultural practices affect populations of farmland birds. Numerous studies have identified lower densities of birds in agricultural areas (Rodenhouse and Best 1994, Chamberlain et al. 2000, Shutler et al. 2000, Ambrosini et al. 2002, Evans et al. 2007, Kirk et al. 2011). Yellowhammer (*Emberiza citronella*) nestlings in agricultural landscapes breed later (Bradbury et al. 2000) and lower insect abundance in these areas is related to lower nestling body condition and foraging intensity (Morris et al. 2005). Invertebrates commonly fed to corn bunting (*Miliaria calandra*) nestlings were negatively correlated with insecticide applications which reduced the probability of nest survival (Brickle et al. 2000). As well, composition of insects in the diet of skylark (*Alauda* arvensis) nestlings is altered by the intensity of agricultural practices (Donald et al. 2001). Thus, agricultural practices can potentially have negative effects on populations of aerial insectivorous birds by reducing insect abundance and diversity.

1.2 STUDY SPECIES

Tree swallows (*Tachycineta bicolor*) are small (~20 g) migratory aerial insectivores that breed throughout central and northern regions of North America (Winkler et al. 2011). Adults arrive on the breeding grounds of Saskatchewan by mid-April and readily occupy nest boxes (Fast 2007, Harriman 2014). Nests are typically located near foraging habitats with a high abundance of insects such as in open areas and near bodies of water (McCarty and Winkler 1999a). Swallows typically initiate clutches in mid-late May, laying ~6 eggs that will hatch after ~14 days of incubation (Winkler et al. 2011, Harriman 2014). One or both adults will feed the nestlings (Quinney and Ankney 1985, McCarty 2002) until they fledge, around 18–22 days post-hatch (Paynter 1954, Stephenson et al. 2009). During the pre-laying period, swallows may forage as far as 10 km from the nest (Dunn and Whittingham 2005) but typically stay closer (<500 m) during egg-laying and chick rearing (McCarty and Winkler 1999a, Stapleton and Robertson 2006). Lower aerial insect abundance is associated with reduced breeding success (Hussell and Quinney 1987) and slower nestling growth (McCarty 2001).Their high reliance on aerial insects — a characteristic of all aerial insectivores — makes swallows an ideal study species for examining potential impacts of habitat alterations such as intensification of agricultural land use on aerial insectivore diet and condition (Ghilain and Bélisle 2008, Calvert 2012). Their biology and diet are well documented, they are highly tolerant to human disturbance and are easy to capture, providing an ideal model species for monitoring and repeated handling.

1.3 STUDY AREAS

I monitored an established tree swallow colony at St. Denis National Wildlife Area (SD). Four additional sites were established during 2012–2014 in landscapes dominated by agriculture

(3 sites) or grassland (1 site). St. Denis National Wildlife Area is located ~40 km east of Saskatoon, Saskatchewan (52.2094 N, -106.0764 W); the site was established in 1990 with 50 nest boxes and now has ~200 nest boxes continuously monitored each season. In 2012, nest boxes were placed ~8 km north of the community of Colonsay, Saskatchewan (COL1; 52.0565 N, -105.9079 W) and ~9.5 km southeast of Burr, Saskatchewan (BUR; 51.9690 N, -105.0756 W). We moved nest boxes ~2 km south of Colonsay 1 in 2013 due to some issues with house wrens (*Troglodytes aedon*) and house sparrows (*Passer domesticus*) occupying nest boxes (COL2; 52.0275 N, -105.9186 W). An additional agricultural site, Humboldt, was added in 2013, located ~10 km west of Humboldt, Saskatchewan (HUM; 52.2021 N, -105.2899 W). In 2014, another reference site was established at Allan (ALA; 51.6257 N, -105.9712 W), approximately 20 km southeast of the town of Allan, Saskatchewan.

Sites differed in their degree of agricultural land use. The grassland site at St. Denis National Wildlife Area is characterized as having over 100 wetlands of varying permanency surrounded by native and planted grasslands and small groves of trees and shrubs in a landscape consisting of cultivated land, tame pasture, and native pasture (Hogan and Conly 1997). At agricultural sites, two to four crop types were typically planted each year and included mostly grains (barley, oats, spring wheat), oilseeds (canola, flaxseed) and pulses (lentils, canary seed, peas), which were less common. Land use at Colonsay 1 was dominated by cropland, with some small areas of tame grassland, and wetlands surrounded by a thick buffer of trees. Colonsay 2 featured large, uninterrupted crop monocultures with several large wetlands (2–3 per quarter section) and trees. The landscape at Burr was dominated by cropland with few trees and experienced landscape conversion over the study period as landowners actively drained wetlands to produce more agriculturally accessible land. Each quarter section had ~5–10 wetlands

surrounded by cattails (*Typha latifolia*) and other emergent vegetation or wetlands were cropped to the edge of the water. Humboldt consisted of numerous wetlands varying from ephemeral ponds to large, permanent bodies of water with little or no vegetative buffer between the water and crop. Finally, the second reference site, Allan, has a mixture of native and non-native grasses, many trees and diverse seasonal and permanent wetlands.

Nest boxes were placed on metal t-bars, 1.5 m above the ground with the entrance facing southeast. Boxes were spaced 30 m apart along fencerows or near the edge of agricultural fields. Two different nest box types were used, "Long Point" (LP; Hussell and Quinney 1987) and "Golondrinas de Las Americas" (GOLO; David Winkler, Cornell University, Ithaca, NY; http://golondrinas.cornell.edu) because they were readily available. Each site had the same GOLO:LP ratio of 25:5 in 2012 and 18:12 in 2013. In 2014, ratios were 15:17 at SD and BUR and 14:18 at COL2, HUM, and ALA. Similar ratios of old and newly constructed nest boxes were used across all sites. The two nest box styles were alternated along the nest box transects to average any nest box effects across a small landscape (~800 m) in proximity to the boxes.

1.4 THESIS OBJECTIVES

My broad goal was to investigate indirect links between agricultural land use and aerial insectivore reproduction and diet through their main prey, aerial insects. If agricultural land use reduces aerial insect abundance or diversity, then I predicted that the reproductive ecology or diet of aerial insectivores could be altered. I specifically examined insect abundances and biomass in response to agricultural land use and potential impacts on tree swallow productivity and nestling body condition (Chapter 2). Using stable isotopes, I evaluated the diet and niche width of tree swallows across areas with varying levels of agricultural land use, and then

examined relationships between assimilated diets and body condition of adults and nestlings (Chapter 3).

1.4.1 Agricultural practices and avian reproductive ecology and body condition

Intensive agricultural practices reduce local biodiversity and as such may impact the abundance of aerial insects that are vital for reproduction in aerial insectivores. Other passerines (blue tits (*Cyanistes caeruleus*); Tremblay et al. 2003), including aerial insectivores (Bryant 1975; Turner 1982; Martin 1987), delay breeding or lower reproductive output with habitat and weather-related reductions in food availability. In Chapter 2, I examined if aerial insect abundance and biomass (dry weight) are negatively impacted by agricultural land use, subsequently affecting components of tree swallow reproductive ecology. I compared insect abundance and biomass among sites of varying agricultural land use. As well, the nest box occupancy rate, timing of breeding and general measures of reproductive performance (i.e., clutch size, brood size, number of fledglings) and nestling body condition were compared. Due to lower biodiversity in agricultural areas, tree swallows may be selecting more pristine, natural habitats for breeding, resulting in lower occupancy rates at agricultural sites relative to reference sites. Aerial insectivores, like swallows, are "income breeders" (Drent and Daan 1980, Winkler and Allen 1996) and rely primarily on current food resources on the breeding grounds for reproduction rather than stored nutrients (i.e., capital breeders). If agricultural land use causes lower insect abundance and biomass, this may delay the timing of breeding, resulting in a later clutch initiation date and subsequently lower reproductive success. Alternatively, reduced insect availability may not affect reproductive timing or success, but could impair adult or nestling body condition. In this thesis, I examined this relationship with nestling body condition only.

1.4.2 Dietary shifts and implications for swallow body condition

Optimal-foraging theory suggests that individuals will forage in a manner to maximize energy intake by selecting the most profitable prey items (Pyke et al. 1977, Krebs and Davies 1987). When abundance of the most preferred prey items is reduced, individuals may shift their diet to another, more abundant, prey item to balance energetic costs associated with longer foraging distances and flight time with the benefits of enhanced nutritional intake. Dietary shifts in farmland birds are related to surrounding habitat (Orlowski and Karg 2012) and the composition of prey available (Girard 2012, Alberts 2013). I used stable isotope analysis in Chapter 3 to compare the proportion of aquatic and terrestrial prey sources in the diet and isotopic niche widths (i.e., variation in diet) of tree swallow adults and nestlings between cropland-dominated agriculture sites and a grassland-dominated reference site. If insect abundance and biodiversity are lowered in agricultural landscapes, I predicted that swallows will shift their diet to less preferred prey items and have larger isotopic niche widths (i.e., more variation) at cropland dominated sites. Increased foraging effort during the nestling period and temporal declines in prey availability through the breeding period may also result in changes in diet. Thus, I compared adult and nestling diets to examine spatiotemporal responses in the diet of tree swallows associated with agricultural land use. Finally, I related the assimilated diet (i.e., isotopic values) of swallows to their body condition to examine if potential dietary shifts in agricultural environments could have long-lasting effects on both adults and nestlings. Overall, tree swallows may respond to agricultural land use by 1) continuing to forage on the same diet as reference sites, but have reduced body condition due to lower insect abundance; or 2) shift their diet to a less preferred, but more available prey source to maintain their body condition.

CHAPTER 2. EFFECTS OF AGRICULTURAL LAND USE ON THE REPRODUCTIVE ECOLOGY OF TREE SWALLOWS (*TACHYCINETA BICOLOR*)

2.1 INTRODUCTION

The intensive alteration of the landscape through changes in agricultural practices encompasses many factors proposed to affect bird populations, such as habitat alteration and degradation and exposure to pesticides. Such agricultural practices focus on shorter crop rotations, reduced crop diversity, increased use of agrochemicals, and removal or degradation of non-farmed habitats such as wetlands, margins, woodlands and hedgerows (Matson et al. 1997, Stoate et al. 2001, Tscharntke et al. 2005). Landscape changes due to agricultural intensification have transformed farms into simpler, homogenous areas with reported negative consequences for biodiversity (Benton et al. 2003, Tscharntke et al. 2005, Batáry et al. 2010). The loss of wetlands and field margins in favour of large fields of monoculture crops negatively affects insect availability (Wilson et al. 1999, Grüebler et al. 2008), whereas agricultural habitats containing grasslands or field margins are likely to enhance insect species richness (Duelli et al. 1999, Di Giulio et al. 2001). Riens et al. (2013) found that the presence of a vegetative buffer around wetlands had a positive effect on invertebrate numbers and diversity of genera, including Diptera species which are a main prey item for the aerial insectivorous species, the tree swallow (*Tachycineta bicolor*) (Quinney and Ankney 1985, McCarty and Winkler 1999a, Mengelkoch et al. 2004, Beck et al. 2013).

Recent declines in many populations of aerial insectivorous bird species are proposed to be due to reductions in their main prey source, flying insects (Calvert 2012). Insectivorous birds frequently occupy farmland habitats where they are highly dependent on abundant insect prey.

Changes in insect availability and the birds' ecology may signal single or multiple interacting factors associated with agricultural practices. For example, reduced aerial insect abundance is associated with lower adult mass (Jones 1987, Møller 2013), poorer breeding success (Hussell and Quinney 1987, Møller 2013) and reduced nestling growth rate (McCarty 2001) in tree swallows. In Europe, abundance of invertebrates in agricultural areas was positively correlated with corn bunting (*Emberiza calandra*) nestling mass (Brickle et al. 2000). Work with barn swallows (*Hirundo rustica*) has shown that livestock farming can provide productive invertebrate habitat in pasture land that birds forage in more than in cereal crop fields (Evans et al. 2007). Both clutch size and annual reproductive success of barn swallows were higher in areas with dairy cattle farming relative to areas without (Møller 2001). With increasing agrochemical use, drainage of wetlands and conversion of semi-natural areas and pastures into productive cropland, aerial insectivores may experience reductions in suitable foraging habitat that supports successful reproduction.

Here, I aim to evaluate potential negative effects from agricultural land use on timing of breeding, reproductive investment and success, and nestling body condition of an aerial insectivore, the tree swallow. Tree swallows are an ideal study species for examining potential impacts of agricultural land use because, like other aerial insectivore species, they are highly reliant on aerial insects. They also have a biology and diet that are well documented, they are attracted to artificial nest boxes, highly tolerant to human disturbance and are easy to capture, allowing for detailed reproductive studies (Jones 2003, Calvert 2012). Given the known effects of agricultural activities, I predict that at agriculturally dominated sites, tree swallows will show lower nest box occupancy, initiate breeding later, reduce clutch size, yield fewer nestlings and/or produce nestlings in lower body condition. I will further explore whether these patterns are

mediated by possible differences in insect biomass and abundance between agricultural and grassland reference sites.

2.2 METHODS

2.2.1 Characterization of Agricultural Land Use

The Canadian Prairies contain 82% of Canada's cropland (over 30 million ha) and use 75% of the fertilizers and 80% of the country's total pesticides (Kissinger and Rees 2009, Statistics Canada 2011). Dominant crop types seeded in the region include non-irrigated varieties of wheat/durum, canola (oilseed rape), lentils and barley. These crop choices differ from eastern Canada which is dominated by corn, soybeans, and wheat (Statistics Canada 2015).

Land use was classified within 3–5 quarter sections (1 quarter section is 0.65 km^2) adjacent to nest boxes (i.e., < 800 m from nest boxes) at six study sites (Burr, Colonsay 1, Colonsay 2, Humboldt, St. Denis, Allan; Appendix 1), which is within the foraging range of swallows during the nesting period (McCarty and Winkler 1999a, Stapleton and Robertson 2006). Three quarter sections were sampled at Allan, four at Colonsay and five at Burr, Humboldt, and St. Denis. Differences in sample sizes were due to logistical constraints as I avoided placing nest boxes in wetlands, road approaches, thick patches of trees, and in close proximity of houses. In each quarter section I calculated the proportion of area that was crop (i.e., grains, oilseed, and pulse crops), grass (i.e., native/non-native grasses, pasture), trees, open water, and infrastructure (i.e., buildings, gravel pits, roads) using orthophoto imagery in ArcMap (ESRI, 2013). Neonicotinoid insecticides are the most commonly applied insecticide seed treatments in the Prairie region, so acetamiprid, clothianidin, thiamethoxam, and imidacloprid were measured (and concentrations summed) in water samples collected from 3–5 wetlands per

site in June each year. Given known sensitivity of aquatic invertebrates to neonicotinoids and adverse effects of this insecticide on their survival, growth and emergence (Morrissey et al. 2015), neonicotinoid concentrations in wetland waters provided another measurement of agricultural intensification. See Main et al. (2014) for further information about water sample collection and pesticide residue analysis. Crops were observed being sprayed with other pesticides but this information was not recorded.

2.2.2 Nest Box Monitoring

Nest boxes were visited every 2 days starting in mid-May to evaluate nest occupancy and timing of breeding. A nest was considered initiated when fresh material was present and at least one egg laid. After the first egg was laid, nests were monitored every day to determine clutch size and approximate onset of incubation (i.e., same number of eggs for three consecutive days). Nest visits commenced again near the projected hatch date (~12–14 days after the last egg was laid) to verify the start and end date of hatch, number of eggs that hatched and, finally, at 18 days post-hatch to determine the number of fledglings. Boxes were re-visited 10 days later to look for new nesting attempts. If no eggs or fresh nesting material were found the nest was removed and the box was cleaned out.

When all eggs had hatched adult swallows were captured in the nest box, banded and measured, usually within 3 days of hatch. At 12 days post hatch, nestlings were banded and measured for the lengths of the wing and 9th primary feather (nearest 0.5 mm with a wing-ruler), head-bill length (nearest 0.01 mm with calipers), and body mass (nearest 0.5 g with a Pesola scale). Adults were sexed (presence of brood-patch for females, presence of cloacal protuberance

for males). Females were aged as second year (SY) or after second year (ASY) based on plumage colouration (Hussell 1983). Unbanded males were aged as after hatch year (AHY).

2.2.3 Invertebrate Collection and Biomass Index

Three passive insect samplers (as previously described by Hussell and Quinney (1987)) were evenly spaced along the row of nest boxes at each site in an open area, as far away as possible from trees and — where possible — on a high point of land. The net is ~2 m above the ground which is within the foraging height (~0–20 m) of tree swallows and captures insects in similar compositions and size classes to those in tree swallow diets (McCarty and Winkler 1999). Quinney and Ankney (1985) found that insects longer that 10 mm only made up 0.7% of insects delivered to nestlings at two tree swallow colonies where insect abundance differed by almost two orders of magnitude. Daily insect abundance and biomass were measured from May through July by passive samplers that funnel aerial insects into jars containing 70% ethanol with 5% glycerol added to slow evaporation of the ethanol and to preserve insects. Samples were transferred and stored in 70% ethanol until they were counted in the lab and dried for 24 hours at 95˚C to determine dry weight biomass. Insects longer than 13 mm were excluded from counts and biomass calculations because they are considered rare in food deliveries to tree swallow nestlings (Quinney and Ankney 1985) and made up less than 0.5% of captured insects from the nets. A daily insect biomass index (IBI) was calculated by dividing the biomass of dry insect sample (g) by the total duration of sample collection period (seconds). This dry weight was then corrected for wind speed by dividing by the mean reported wind speed (m/s) during the time of sample collection (expressed as g dry biomass/m * 10^6). Hourly wind speed data were obtained from the nearest Environment Canada weather stations. An anemometer was also placed at each passive net for a minimum of two weeks during the field season and the local wind speed was

used to determine a correction equation for reported wind speeds from Environment Canada weather stations because the distances from study sites to weather stations varied (~1–70 km).

In 2013, standardized terrestrial invertebrate net sweeps were completed at three time periods: 1) when the majority of females within the population had begun incubation; 2) peak hatch; 3) when the majority of the nestlings reached 12 days of age. Terrestrial sweeps were performed in three habitats: 1) upland; 2) along the nest box transect in the ditch; and 3) in wetland vegetation (wet meadow and emergent wetland zones). Swallows are routinely observed feeding in open habitats and over water bodies (McCarty and Winkler 1999a, Michelson, personal observation); thus, I assumed that the habitats chosen would represent the insect community potentially available to foraging swallows. To maintain standardization between habitats and sites, each transect was swept 150 times, at various depths within the vegetation, with a 15 cm diameter butterfly net. Each transect was completed within 3–4 minutes. All transect sweeps were conducted into the wind at wind speeds < 25 km/hr. All sweeps were completed when minimum temperature exceeded 18.4˚C, when aerial insects are more active (Winkler et al. 2013).

2.2.4 Statistical Analyses

2.2.4.1 Classification of Study Sites

To classify each study site with respect to agricultural intensity characteristics, I performed a principal component analysis (prcomp, package *stats*, R version 3.1.0; R Core Team 2013) of measurements of the areas (m^2) of crop, grass, trees, water, infrastructure, and mean total neonicotinoid concentrations. Land use data were standardized and mean-centered prior to analysis. A multiple comparison of means among study sites using Tukey contrasts of PC1 were

used (glht, package *multcomp*, R version 3.1.0) to group study sites based on dominant landscape features.

2.2.4.2 Nest Box Occupancy and Breeding Biology

Nest box occupancy rates were compared with G-tests. To examine effects of agricultural land use on clutch initiation date, clutch size (clutch model), brood size (brood model), and number of fledglings (fledge model), I ran generalized linear models (glm, package *stats*, R version 3.1.0) with a Poisson distribution and log link function. Explanatory variables included year, land type (land; agricultural or reference study sites), female prior breeding experience (f.recap) and nest box type (box.type). Clutch initiation date (CID) was included in the clutch, brood, and fledge models as Pearson's correlations (cor.test, package *stats*, R version 3.1.0) show that each of these responses are negatively correlated with CID (clutch size: $r = -0.46$, $p < 0.0001$; brood size: $r = -0.31$, $p < 0.0001$; number fledged: $r = -0.20$, $p = 0.0004$; $n = 304$ nests for all correlations). Interactions among year, land type, and clutch initiation date (clutch, brood and fledge models) were included as explanatory variables. Additional models were run for clutch initiation date to justify the use of a Poisson distribution. I completed two general linear models, one with a Gaussian distribution and the other with a Poisson distribution of clutch initiation date against the global model (year * land + box.type + f.recap). Model fit (of the residuals) was substantially improved with the Poisson model and violations of homogeneity removed, validating the chosen method. Older females initiate egg laying earlier and typically have higher reproductive success than yearling females (Forslund and Pärt 1995, Robertson and Rendell 2001, Hatch and Westneat 2007). Newly established sites limited me to aging the females as either "second year" (SY; known to have hatched in the preceding calendar year) or "after second year" (ASY; known to have hatched earlier than the preceding calendar year or

year of hatch unknown). Although female age could not be included as a variable in the models, female experience at a site could be used as a proxy of age under the assumption that birds marked previously as adults are more experienced with local conditions than unmarked adults. Different nest box designs and wood thickness can also have effects on the internal microclimate (Lambrechts et al. 2010). Thick-walled nest boxes have significantly lower variation in daily temperature (Fairhurst et al. 2012). More extreme temperatures in thin-walled nest boxes could negatively affect fledgling success (Ardia 2013). As well, experimentally controlling the nest box microclimate to reduce temperature variability increased survival of nestlings (Dawson et al. 2005). Due to these potential impacts on swallow reproduction and nestling quality and survival, nest box type was included as a variable in all models.

The above models tested clutch initiation date between the two land types. However, the distribution of clutch initiation dates between land types could also provide information on the breeding ecology of tree swallows. Initiation of breeding in passerines may depend on environmental conditions and the parent's ability and experience to gather nutrients (particularly calcium) for egg production (Perrins 1970; Drent and Daan 1980; Turner 1982); thus, the distribution in the timing of breeding may indicate differences in parental quality and/or food quantity and quality between land types. As well, intra- and interspecific competition may be greater at agricultural sites due to expected lower insect abundances, forcing some individuals to forage longer (days) to meet energy required for egg production. Two-sample Kolmogorov-Smirnov tests (ks.test, package *stats*, R version 3.1.0) were used to examine potential differences in the seasonal distribution of clutch initiation date (CID) between agricultural and reference sites for each year, separately.

2.2.4.3 Nestling Body Condition

Pearson correlations revealed strong correlations between the lengths of the wing and 9th primary feather ($r = 0.94$, $p < 0.0001$), the wing and head bill ($r = 0.7$, $p < 0.0001$) and the 9th primary feather and head bill ($r = 0.64$, $p < 0.0001$). To account for collinearity among these variables a principal component analysis of the structural measurements of all nestlings was conducted. Principal component (PC) 1 accounted for 84% of the variation in the structural measurements. Some nestlings were not measured at 12 days post-hatch and age at measurement was significantly correlated with PC 1 ($r = -0.38$, $p < 0.0001$, $n = 1655$). The residuals of mass regressed against PC1 and nestling age at measurement were used as an index of nestling body condition (nBCI). Linear mixed effects models (lme, package *nlme*, R version 3.1.0) were used to examine effects of land type on nBCI of 1655 nestlings from 280 nest boxes. Year, clutch initiation date (CID), brood size, female experience (f.recap) and nest box type (box.type) were included as fixed effects. Potential interactions between year, land type and CID were considered. Nest box identification was included as a random effect to account for the "clustering" of nestlings within nest boxes.

2.2.4.4 Aerial Insect Abundance and Biomass from Passive Aerial Insect Samplers

Values of mean daily IBI and insect abundance at each site were log transformed prior to analyses to improve normality. Generalized least square models (gls, package *nlme* , R version 3.1.0) controlling for year and date (mean-centered) were run with an autoregressive correlation structure with 1 day lag (AR-1) to examine differences in daily IBI and abundance between agricultural and reference sites at three times during tree swallow breeding: clutch initiation, egg laying, and nestling periods. Explanatory variables included year, date, land type and two way interactions between the three variables. The period of clutch initiation is defined as from the 10th percentile to the 90th percentile of CID in each year. Similarly, the egg laying period

extended from one day before the 10th percentile of CID to the 90th percentile of last egg within each year and the nestling period spanned from the 10th percentile of hatch to 18 days after the 90th percentile of hatch.

2.2.4.5 Insect Abundance from Terrestrial Net Sweeps

Collections from terrestrial net sweeps were identified to order. I focused on the Diptera order as they encompass a large majority of the captures from the passive nets and previous work across multiple habitats has shown Diptera to be the most consumed order (50-75%) by tree swallows (McCarty and Winkler 1999a, Mengelkoch et al. 2004, Beck et al. 2013). Diptera species were further classified, with midges (Chironomidae) and mosquitos (Culicidae) assumed to be of aquatic or semi-aquatic life cycle (hereafter, aquatic Diptera) and all other Diptera were considered terrestrial Diptera. I examined potential differences in insect abundance of aquatic and terrestrial Diptera, separately, using linear mixed effects models (lme, package *nlme* , R version 3.1.0). Abundances were log transformed prior to analysis. Fixed effects included land type (agricultural or reference study sites), habitat (upland, wetland, and ditch) and time period (incubation, hatch, 12 days post-hatch) and sampling date was included as a random effect.

2.2.4.6 Model Selection

Information-theoretic approaches (Akaike's Information Criterion for small sample sizes; AIC_c; Burnham and Anderson 2002) were used to compare models to determine relative support for a variable's influence on the above tested responses (aictab, *AICcmodavg*, R version 3.1.0). Models within 2 AIC units were considered competitive. An intercept-only model (statistical null) was included in candidate model sets. Models were run using maximum likelihood

estimation to determine the best-approximating model. Parameter estimates (± SE) from best-approximating models were acquired using restricted maximum likelihood estimation.

2.3 RESULTS

2.3.1 Characterization of Agricultural Land Use

Principal component 1 and 2 accounted for 63% of the variation in landscape composition (37% and 25%, respectively; Figure 2.1). Positive PC1 values are related to greater area of cropland and higher neonicotinoid concentrations while negative PC1 values are related to greater area of grass, water, and trees (Table 2.1). More negative PC2 values were related to higher neonicotinoid concentrations and water and while greater areas of grass, trees and crop were associated with more positive PC2 values. The amount of crop and neonicotinoid concentrations were likely not correlated because Humboldt had more water than the other agricultural sites and neonicotinoids were sampled in the water. As well, concentrations were much higher at Humboldt (mean = 361 ng/L) than at other crop dominated sites (mean = 49 ng/L). As expected, *post-hoc* Tukey contrasts of PC1 grouped the cropland-dominated sites, Burr, Colonsay1, Colonsay 2 and Humboldt, together and the grassland dominated sites, Allan and St. Denis together (Figure 2.1). PC2 scores were significantly different between Humboldt and Colonsay 1 (β = 2.82, S.E. = 0.58) and Humboldt and St. Denis (β = 1.75, S.E. = 0.55). This is likely due to variation in neonicotinoid concentrations. All further analysis which used land type (land) as an explanatory variable is based on results of PC1 where land has two levels, agriculture (cropland) and reference (grassland). When examining tree swallow responses by site, Colonsay 1 and Colonsay 2 were subsequently combined to represent one site, and referred to as Colonsay (COL), because the sites were both classified as agricultural and had similar PC1

(β = 0.92, S.E. = 0.4, p = 0.2) and PC2 (β = 0.90, S.E. = 0.61, p = 0.69) scores. Furthermore, swallows previously banded at Colonsay 1 in 2012 were recaptured at Colonsay 2 in 2013 and 2014 and year was not an important factor in explaining the responses of tree swallow reproduction and condition (details below).

Table 2.1. Variable loadings of principal component 1 (PC1) and 2 (PC2), percent of variation explained by each axis and cumulative variation from a principal component analysis of land use classes at 6 tree swallow study sites, Saskatchewan.

Land Use Class	PC1	PC2
Crop	0.61	0.29
Neonicotinoids[1]	0.28	-0.62
Grass	-0.59	-0.03
Trees	-0.29	0.12
Water	-0.16	-0.66
Infrastructure[2]	-0.30	-0.29
% Variation	0.37	0.25
Cumulative Variation	0.37	0.63

[1] Mean total neonicotinoid concentration in wetland water.
[2] Includes building, roads, gravels pits.

2.3.2 Breeding Biology

Nest box occupancy could not be formally tested because all sites had similar occupancy rates and models would not converge. Although nest box occupancy tended to be lower on agricultural sites when compared with the reference site at St Denis, this could be attributed in large part to low occupancy in the year that sites were first established (Table 2.2). By 2014, occupancy approached 100% on all agricultural sites.

The null model explained more variation in clutch initiation date than the explanatory variables tested (Table 2.3; Appendix 2). Similarly, I obtained no support for the predicted

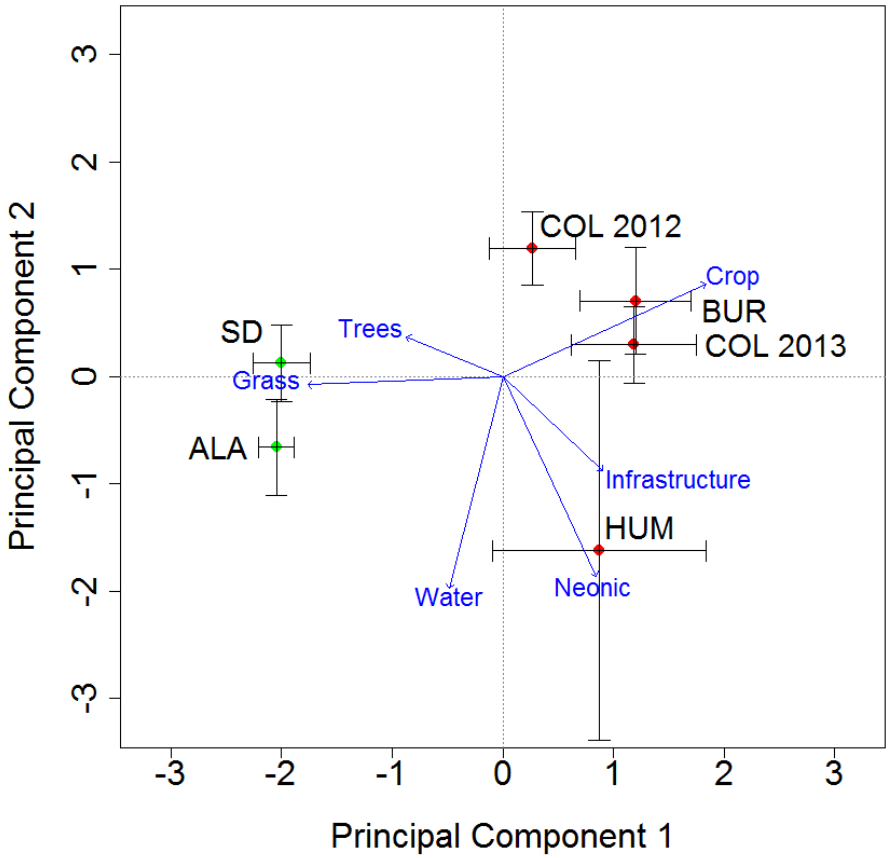

Figure 2.1. Mean ± S.D. of principle component 1 and 2 of the area/quarter section under different land use classes: crop, grass (native and non-native grasses and pasture), infrastructure (i.e., all roads, buildings, gravel pits), trees, open water and mean total neonicotinoid concentrations in wetlands. Reference sites are in green (Allan (ALA), St. Denis (SD)) and agricultural sites are in red (Burr (BUR), Colonsay 1 (COL 2012), Colonsay 2 (COL 2013), and Humboldt (HUM)).

negative effect from agricultural land use on clutch size, brood size, and number of nestlings fledged. Clutch initiation date is the best predictor of those responses (Table 2.3; Appendix 2). With advancing clutch initiation date there was a decline in clutch size (β = -0.01, S.E. = 0.004), brood size (β = -0.01, S.E. = 0.004) and number of fledged nestlings (β = -0.01, S.E. = 0.004). Experienced females fledged more young than yearling females (β = 0.10, S.E. = 0.05).

Table 2.2. Summary of the reproductive productivity of tree swallows at 3–5 sites in south-central Saskatchewan, 2012–2014. The mean ± S.D. of clutch initiation date (CID), clutch size, brood size, number of nestlings fledged, proportion of eggs that hatched and proportion of hatched chicks that fledged are reported. Site-year refers to the number of years since nest boxes were placed on the site.

Year	Land Type[1]	Site[2]	Site-Year	Occu. (%)[3]	N_f[4]	SY Females (%)[5]	Exp. Females (%)[6]	N[7]	CID	Clutch Size	Nestlings Hatched	$\hat{p}$ hatched[8]	Nestlings Fledged	$\hat{p}$ fledged[9]
2012	AG	BUR	1	57	15	47	0	18	151.2 ± 8.9	6.1 ± 1.1	5.0 ± 1.8	0.79 ± 0.25	4.5 ± 2.4	0.85 ± 0.34
		COL	1	70	21	47	0	22	150.1 ± 5.5	6.3 ± 1.2	5.7 ± 1.6	0.88 ± 0.22	5.6 ± 1.6	0.97 ± 0.06
	REF	SD	23	100	31	6	32	31	149.4 ± 5.5	6.8 ± 0.7	5.9 ± 1.6	0.87 ± 0.21	5.3 ± 2.1	0.90 ± 0.26
2013	AG	BUR	2	83	25	0	16	25	148.5 ± 6.4	6.6 ± 0.7	6.0 ± 1.2	0.90 ± 0.12	5.4 ± 2.0	0.90 ± 0.28
		COL	2	73	21	5	19	22	150.8 ± 7.1	6.0 ± 1.4	4.6 ± 2.3	0.73 ± 0.34	4.5 ± 2.3	0.98 ± 0.07
		HUM	1	40	13	8	0	13	153.5 ± 12.6	6.3 ± 1.1	5.8 ± 1.4	0.91 ± 0.11	4.7 ± 2.5	0.81 ± 0.37
	REF	SD	24	100	30	0	40	31	147.9 ± 5.3	6.8 ± 0.8	6.1 ± 1.6	0.89 ± 0.21	5.9 ± 1.8	0.97 ± 0.14
2014	AG	BUR	3	100	32	0	38	32	149.3 ± 2.1	6.7 ± 0.5	6.2 ± 1.0	0.92 ± 0.11	5.9 ± 1.1	0.96 ± 0.12
		COL	3	94	30	0	40	31	149.7 ± 5.4	6.6 ± 0.9	6.0 ± 1.6	0.90 ± 0.22	5.6 ± 2.2	0.93 ± 0.25
		HUM	2	100	32	3	22	32	149.6 ± 4.7	6.8 ± 0.7	6.4 ± 1.0	0.90 ± 0.20	6.1 ± 1.5	0.92 ± 0.25
	REF	SD	25	100	32	0	84	33	148.3 ± 4.9	6.8 ± 0.7	6.1 ± 1.4	0.91 ± 0.19	6.0 ± 1.5	0.97 ± 0.08
		ALA	1	75	23	39	0	23	152.5 ± 9.5	5.9 ± 0.9	5.3 ± 1.3	0.89 ± 0.17	4.7 ± 1.9	0.90 ± 0.29

[1] Dominant land cover. Agriculture (AG) is cropland; reference (REF) is grassland.

[2] Site names: Allan (ALA), Burr (BUR), Colonsay (COL), Humboldt (HUM), St. Denis NWA (SD).

[3] Percentage of nest boxes occupied.

[4] Number of females captured.

[5] Percentage of second year (SY), or yearling, females.

[6] A female is experienced if it was previously banded

[7] Number of nest boxes where a nest was initiated (nesting material with 1 egg laid).

[8] Calculated as the brood size at hatch divided by the clutch size.

[9] Calculated as the number of nestlings that fledged divided by the brood size at hatch.

Timing of clutch initiation ranged from 20 May to 23 June in 2012, 21 May to 29 June in 2013 and 23 May to 28 June in 2014 with 95% of nests initiated by 4 June each year. The distribution of CID was similar between agricultural and reference sites in 2012 ($D = 0.11$, $p = 0.99$) and 2013 ($D = 0.14$, $p = 0.83$) but a trend for clutch initiation to be more synchronous at agricultural sites than references sites was seen in 2014 ($D = 0.22$, $p = 0.07$). However, this relationship was principally driven by asynchronous breeding at the newly-established Allan reference site.

2.3.3 Nestling Body Condition

Mean (± S.D.) body condition index of nestlings (nBCI) was -0.15 ± 1.70 at agricultural sites and 0.24 ± 1.52 at reference sites (Figure 2.2). After controlling for effects of clutch initiation date, brood size, and nest box type, 12-day-old nestlings from the reference sites had higher body condition than those at agricultural sites (Table 2.4; Appendix 2; $\beta = 0.31$, S.E. = 0.14). Nest box type was also a strong predictor of nestling body condition; nestlings produced in GOLO nest boxes had higher nBCI than those raised in LP nest boxes ($\beta = 0.48$, S.E. = 0.14). Nestling body condition remained consistent or declined with advancing CID but this relationship showed a stronger decline (steeper) as brood size increased (CID x brood size: $\beta = -0.02$, S.E. = 0.01). There was considerable inter-annual variation in nestling body condition among sites of the same land type (Figure 2.3). For example, in 2012 and 2014, nestlings at Colonsay (agriculture) had the lowest body condition — whereas in 2013, Humboldt (agriculture) nestlings were lowest.

Table 2.3. Model selection results for the responses, clutch initiation date (CID), clutch size, brood size and number of nestling fledged for tree swallows at 3–5 sites in south-central Saskatchewan (2012: n = 3 sites; 2013: n = 4; 2014: n = 5) using generalized linear models with a Poisson error distribution. Only the top models with $\Delta AIC_c < 2$ and the intercept-only model (null) are presented.

Response	Model Structure[1]	K[2]	AIC_c[3]	ΔAIC_c[4]	Deviance[5]	w_i[6]
CID	null	2	2104.19	0.00	2102.18	0.30
	f.recap	3	2106.00	1.81	2101.96	0.12
	land	3	2106.05	1.86	2102.02	0.12
	box type	3	2106.13	1.94	2102.08	0.11
Clutch Size	CID	3	1168.57	0.00	1164.52	0.28
	CID + f.recap	4	1170.29	1.73	1164.22	0.12
	null	2	1173.43	4.86	1171.42	0.02
Brood Size	CID	3	1189.07	0.00	1185.02	0.24
	CID + f.recap	4	1190.26	1.20	1184.18	0.13
	CID + box.type	5	1190.98	1.91	1184.90	0.09
	null	2	1194.79	5.72	1192.78	0.01
Number of Nestlings Fledged	CID + f.recap	4	1279.44	0.00	1273.36	0.24
	land + CID + f.recap	5	1280.94	1.51	1272.82	0.11
	CID	3	1281.32	1.89	1277.28	0.09
	CID + box.type + f.recap	5	1281.40	1.96	1273.26	0.09
	null	2	1285.96	6.52	1283.94	0.01

[1] Explanatory variables include year of study (year), agricultural treatment (land; agricultural vs. reference), nest box design (box.type), female experience (f.recap) and interactions among year, agricultural treatment, and clutch initiation date (clutch, brood, fledged models only).

[2] Number of estimable parameters.

[3] Akaike's Information Criterion for small sample sizes.

[4] Difference in AIC_c between each model and the model with the lowest AIC_c value.

[5] -2 × log likelihood.

[6] Model weight.

Table 2.4. Model selection results for body condition index of tree swallow nestlings (nBCI) from 3–5 sites (2012: n = 3 sites; 2013: n = 4; 2014: n = 5) in south-central Saskatchewan using linear mixed effects models with box ID as a random effect to account for multiple nestlings being reared in one box. Only models with $\Delta AIC_c < 2$ and the intercept -only model (null) are presented.

Model Structure[1]	**K**[2]	**AIC_c**[3]	**ΔAIC_c**[4]	**Deviance**[5]	**w_i**[6]
land + CID + brood + box.type + CID × brood	8	5795.14	0	5779.06	0.15
year + land + CID + brood + box.type + CID × brood	10	5795.90	0.76	5775.76	0.10
land + CID + brood + box.type	7	5796.54	1.39	5782.48	0.07
year + land + CID + brood + box.type	9	5796.73	1.59	5778.62	0.07
land + CID + brood + box.type + f.recap + CID × brood	9	5797.04	1.90	5778.92	0.06
null	3	5820.19	25.04	5814.18	0.00

[1] Explanatory variables included year of study (year), agricultural treatment (land; agricultural vs. reference), clutch initation date (CID), brood size (brood), nest box design (box.type), female experience (f.recap) and interactions among these variables.

[2] Number of estimable parameters.

[3] Akaike's Information Criterion for small sample sizes.

[4] Difference in AIC_c between each model and the model with the lowest AIC_c value.

[5] -2 × log likelihood.

[6] Model weight.

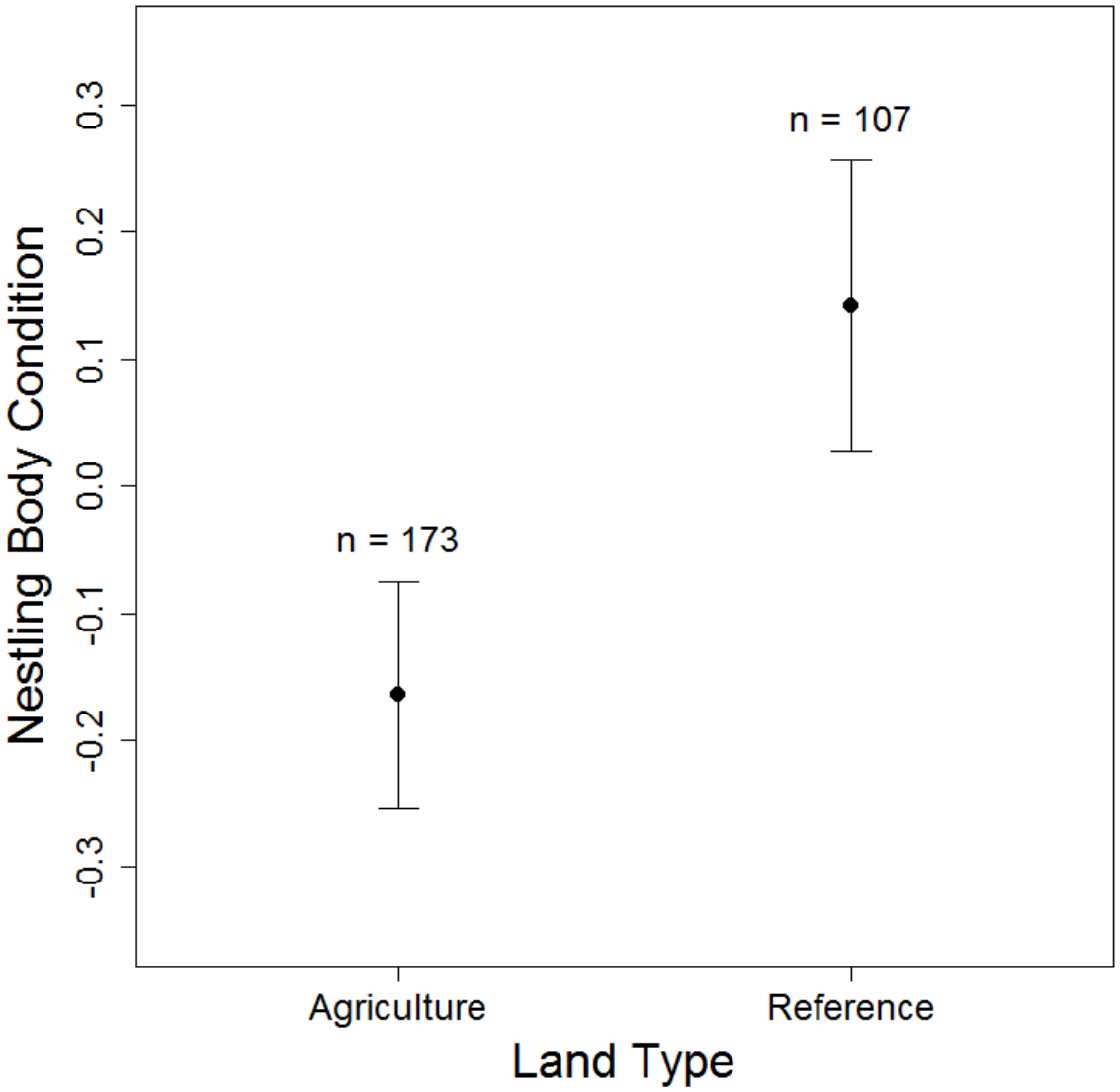

Figure 2.2. Nestling body condition index (least-squares mean ± S.E.) by land type across 3–5 tree swallow sites in south-central Saskatchewan averaged over 2012–2014 (n is number of nest boxes). Means controlled for effects of clutch initiation date, brood size, and nest box type in a linear mixed effects model.

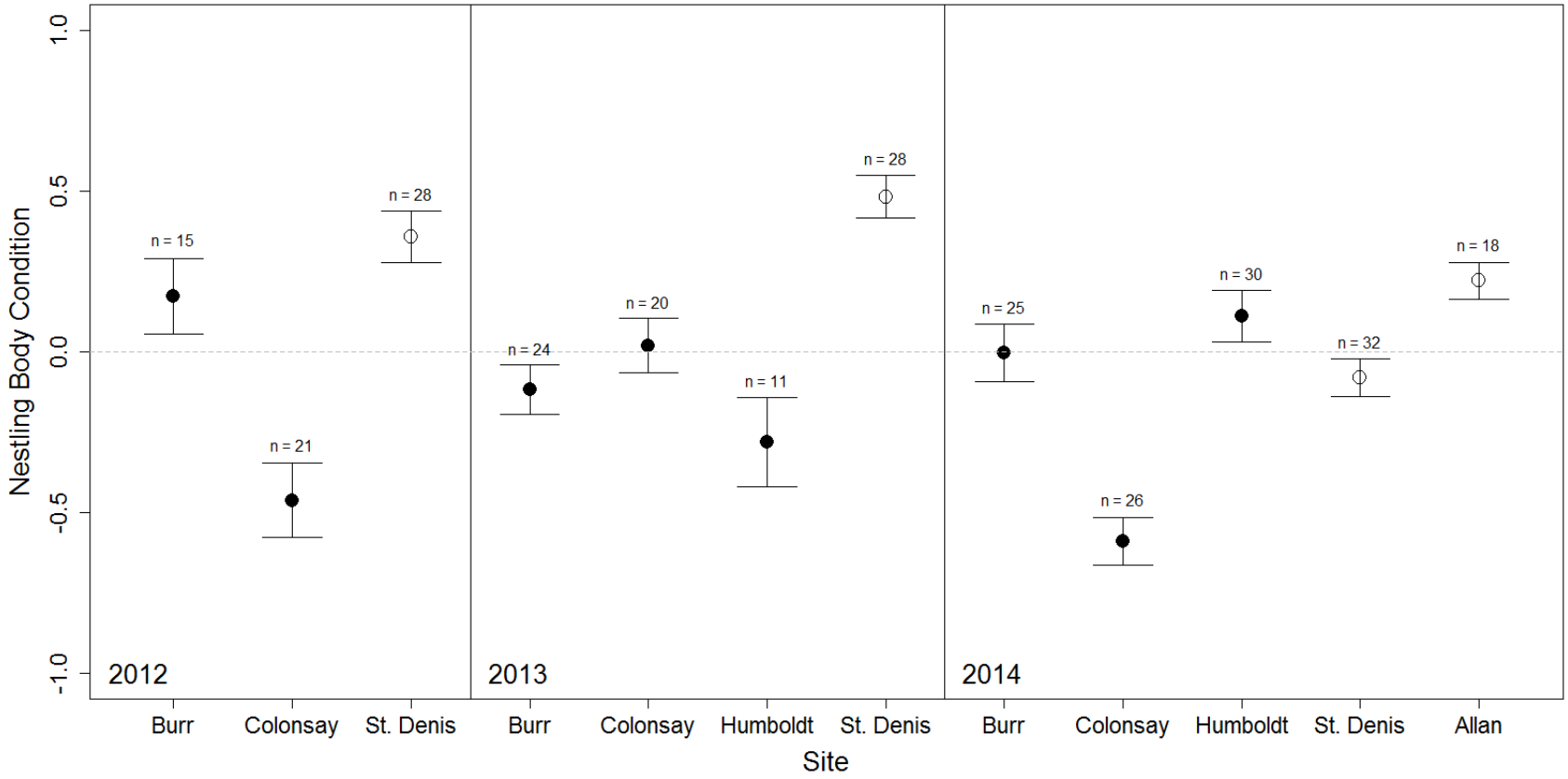

Figure 2.3. Nestling body condition index (least-squares mean ± S.E.) at 3–5 tree swallow sites in south-central Saskatchewan from 2012–2014. Values were adjusted for effects of clutch initiation date, brood size, and nest box type. Sample size (n) is number of nest boxes. Closed circles (●) signify agricultural sites and open circles (○) represent reference sites.

2.3.4 Invertebrate Prey

2.3.4.1 Passive Samplers

Effects of land type on insect abundance and biomass index (IBI) were variable. Land type had an effect on insect abundance during clutch initiation and the nestling period and on IBI during the nestling period (Table 2.5; Appendix 3). Land type did not explain IBI during clutch initiation and egg laying or insect abundance during egg laying and these responses will not be further discussed because of a lack of an effect from agriculture land use. The relationship between land type and insect abundance during clutch initiation was opposite of my prediction as a trend for higher abundance at agricultural sites than reference sites was found (Table 2.6). An interaction between year and date showed that abundance increased with the advancement of date and the increase was greatest in 2014, followed by 2013 then 2012.

Insect abundance began to decline with date, later, during the nestling period and was also higher at agricultural sites than reference sites (Table 2.6; Appendix 3). During this period abundance was highest in 2014, followed by 2013 and 2012 and was stable with date in 2014 but declined at similar rates between 2012 and 2013 (Table 2.6). Consistent with abundance, insect biomass during the nestling period was higher at agricultural sites than reference sites and declined with date (Table 2.6). Estimates were the lowest in 2012 and were similar between 2013 and 2014. Again, a year by date interaction showed relatively stable values over the nestling period in 2014, but declined at similar rates in 2013 and 2012.

Table 2.5. Model selection results of insect biomass index (IBI) and insect abundance in passive aerial nets during three periods of tree swallow reproduction using generalised least-squares models with an auto-regressive with 1 day lag (AR-1) correlation structure at 3–5 sites in south-central Saskatchewan over three years (2012: n = 3 sites; 2013: n = 4; 2014: n = 5). Only the tops models with $\Delta AIC_c < 2$ and the intercept-only model (null) are presented.

Time Period	Response	Model Structure[1]	K[2]	AIC_c[3]	ΔAIC_c[4]	Deviance[5]	w_i[6]
Clutch Initiation	IBI	year + date + year × date	8	555.54	0.00	538.86	0.54
		year + land + date + year × date	9	557.14	1.60	538.30	0.24
		null	3	670.75	115.21	664.64	0.00
	Abundance	year + land + date + year × date	9	374.99	0.00	356.14	0.41
		year + date + year × date	8	376.17	1.19	359.50	0.23
		year + land + date + year × date + land × date	10	376.50	1.51	355.46	0.19
		null	3	533.96	158.97	527.84	0.00
Egg Laying	IBI	year + date	6	494.7	0.00	482.24	0.47
		null	3	524.62	29.92	518.5	0.00
	Abundance	year + date	6	388.53	0.00	376.06	0.30
		year + land + date	7	390.39	1.86	375.78	0.12
		year + land + date + land × date	8	390.47	1.95	373.68	0.12
		null	3	400.08	11.55	393.96	0.00
Nestling Period	IBI	year + land + date + year × date	9	881.80	0.00	863.22	0.36
		year + date + year × date	8	882.72	0.92	866.26	0.23
		year + land + date + year × land + year × date	11	883.53	1.73	860.66	0.15
		null	3	949.56	67.76	943.48	0.00
	Abundance	year + land + date + year × date	8	686.78	0.00	668.20	0.50
		year + land + date + year × date + land × date	9	688.68	1.91	667.96	0.19
		null	2	777.8	91.12	771.82	0.00

[1] Explanatory variables included year of study (year), agricultural treatment (land; agricultural vs. reference) and date (mean-centered) and interactions among these variables.

[2] Number of estimable parameters.

[3] Akaike's Information Criterion for small sample sizes.

[4] Difference in AIC_c between each model and the model with the lowest AIC_c value.

[5] -2 × log likelihood.

[6] Model weight.

Table 2.6. Parameter estimates and S.E. for variable in log scale of variables from the best-approximating models explaining insect abundance or biomass (IBI) during clutch initiation and the nestling period at 3-5 tree swallow sites in south-central Saskatchewan from 2012-2014. Only models that included land type as a predictor variable are shown.

Time Period	Response	Variable	Estimate	S.E.
Clutch Initiation	Abundance	Intercept[1]	3.63	0.23
		2013	0.04	0.27
		2014	-0.61	0.29
		date	0.19	0.15
		reference	-0.45	0.27
		2013 × date	0.77	0.24
		2014 × date	0.92	0.21
Nestling Period	Abundance	Intercept[1]	2.74	0.15
		2013	0.52	0.18
		2014	1.00	0.18
		date	-0.60	0.12
		reference	-0.62	0.16
		2013 × date	-0.02	0.17
		2014 × date	0.58	0.16
Nestling Period	IBI	Intercept[1]	-2.07	0.22
		2013	0.87	0.28
		2014	0.87	0.27
		date	-0.79	0.17
		reference	-0.39	0.24
		2013 × date	-0.05	0.26
		2014 × date	0.67	0.23

[1] Intercept subsumes the baseline estimates of year 2012, agriculture, and year 2012 × date

2.3.4.2 Terrestrial Sweeps

Abundances of aquatic Diptera collected from sweep net samples in 2013 were best explained by land type, habitat, and time period (Table 2.7; Appendix 4). The reference site, St. Denis, had higher abundances of aquatic dipterans (least-square mean ± S.E.) = 1448.18 ± 1.48 individuals/sample) than the agricultural sites (537.18 ± 1.66; Figure 2.4). More aquatic dipterans were captured in ditch habitat (least-square mean ± S.E.) = 537.18 ± 1.66) than in wetland (444.51 ± 1.48) and upland (123.30 ± 1.46) habitats. Abundance was highest during incubation (least-square mean ± S.E.) = 537.18 ± 1.66) and declined through hatch (331.62 ± 1.81) and nestling (82.13 ± 1.71) periods.

Table 2.7. Model selection from linear mixed effects models comparing abundances (log-transformed) of aquatic and terrestrial Diptera collected among four sites classifed as a reference or agricultural site. Sampling date was used as a random effect. Only the top models with $\Delta AIC_c < 2$ and the intercept-only model (null) are presented.

Response	Model Structure[1]	K[2]	AIC_c[3]	ΔAIC_c[4]	Deviance[5]	w_i[6]
Aquatic Diptera	land + habitat + sample period	8	93.38	0.00	70.18	0.75
	null	3	107.40	14.02	100.44	0.00
Terrestrial Diptera	land + habitat	6	136.81	0.00	122.70	0.58
	habitat	5	138.11	1.30	126.64	0.30
	null	3	164.60	27.79	158.04	0.00

[1] Explanatory variables included land type, habitat and sample period.
[2] Number of estimable parameters.
[3] Akaike's Information Criterion, corrected for small sample sizes.
[4] Difference in AIC_c between each model and the model with the lowest AIC_c value.
[5] -2 × Log Likelihood.
[6] Model weight.

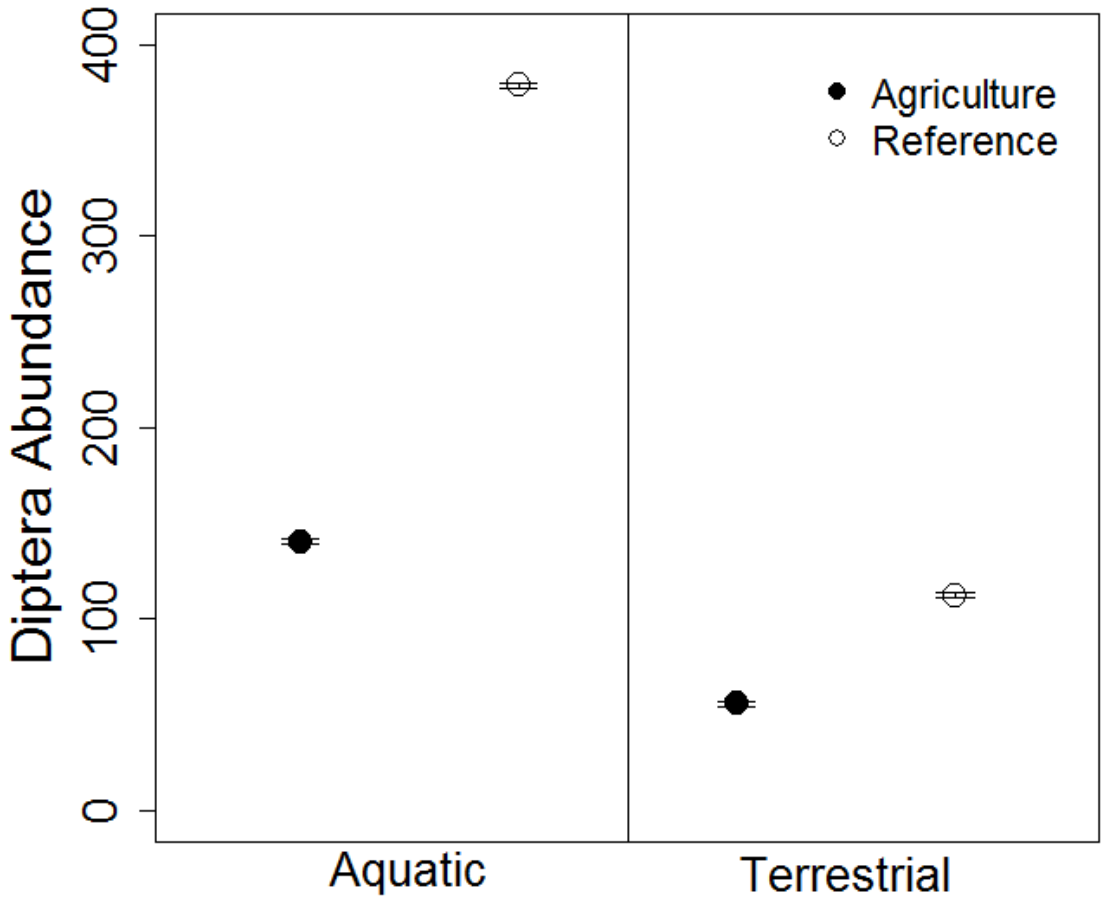

Figure 2.4. Mean abundance per sample (± S.E.) of aquatic (left) and terrestrial (right) Diptera collected by sweep-net at four sites in 2013, after controlling for date and habitat. Sweep-netting was repeated three times during the tree swallow nesting season (incubation until nestlings were 12 days old) at each site and in three habitats for a total of 81 terrestrial sweeps transects at agricultural sites and 28 at St. Denis (reference site).

Land type and habitat best explained abundances of terrestrial Diptera (Table 2.7; Appendix 4). Again, the reference site, St. Denis, had a higher abundance (least-square mean ± S.E.) = 110.22 ± 1.44 individuals/sample) than agricultural sites (54.47 ± 1.35; Figure 2.4). Higher abundances of terrestrial Diptera were captured in wetland habitat (least-square mean ± S.E.) = 159.16 ± 1.36), followed by ditch (54.47 ± 1.35) then upland (19.86 ± 1.35) habitats.

2.4 DISCUSSION

2.4.1. Reproductive Productivity

Although predicted to negatively affect tree swallow reproductive timing and success, effects of agricultural land use were not detected. Nest box occupancy was low in the year a site was established; however, occupancy was not lower at agricultural sites relative to reference sites (grassland). Birds initiated clutches relatively synchronously on all sites. Variation in clutch sizes, brood sizes and numbers of fledglings was largely explained by timing of breeding, not by agriculture land. Previous studies have found that timing of breeding and clutch size in tree swallows is strongly related to food abundance during initiation whereby swallows do not initiate clutches to synchronize nestling growth periods with seasonal peaks in food abundances (Hussell and Quinney 1987, Winkler and Allen 1996, Nooker et al. 2005, Dunn et al. 2011, LeClair 2012). This is possibly because females cannot predict future insect availability (Hussell and Quinney 1987). Studies have identified a positive relationship between insect abundance and clutch size in tree swallows but this relationship likely levels out at higher clutch sizes (5-8 eggs, depending on study site) (Hussell and Quinney 1987, Winkler et al. 2014). Greater proportion of intensive agriculture in the landscape resulted in clutch size reductions of 0.8 eggs in eastern Canada, likely the result of decreased insect availability (Ghilain and Bélisle 2008). Thus, if

agricultural landscapes do reduce insect abundance, it would need to be quite severe to influence clutch size and subsequent productivity measures.

My results are consistent with that reported for another aerial insectivore species, the barn swallow, which did not change timing of breeding or show lower breeding success across sites with various farming practices (Møller 2001). In my study, tree swallow timing of breeding and reproduction was not strongly affected by agricultural land use, suggesting that current agricultural practices in south-central Saskatchewan may not affect insect abundance, or swallows are compensating for differences in food supply. Weather and aerial insectivore prey availability are indirectly related as insect flight activity is reduced at low temperatures, affecting insect availability and delaying the onset of breeding (Taylor 1963, O'Connor and Morgan 1982, Turner 1982a, Saino et al. 2004). There was little variation in the daily temperature and rainfall between my study sites (Michelson, unpublished data) as they were geographically similar (i.e., similar latitudes, ~80 km apart). Additional environmental variables such as wetland depth has been previous found to indirectly affect female swallow clutch sizes at St. Denis. In years with greater wetland depth and higher aerial insect biomass, swallows produced larger clutches (Fast 2007). Since 2011, Saskatchewan has experienced extensive flooding which potentially increased wetland persistence and depth across all sites, favouring higher insect production. I speculate that an effect from agricultural land use may be detected in drier years due to confounding impacts of reduced aquatic habitats and higher application of pesticides to counter insect pest outbreaks from warm and dry conditions (Rosenzweig et al. 2001). Spring droughts have negative effects on arthropods eaten by aerial insectivores (Frampton et al. 2000). These impacts could persist throughout the breeding season and subsequent fall migration which may lead to long-term impacts on survival and population size.

2.4.2 Nestling Body Condition

Tree swallow nestlings achieve higher body condition and grow faster when insect abundance is high (Quinney et al. 1986, McCarty and Winkler 1999a). Nestlings raised on agricultural sites had consistently lower body condition than those at St. Denis (i.e., reference). During the first year Allan site (reference) was established, adults produced nestlings with a higher mean body condition than nestlings from the well-established agricultural site, Colonsay. Indirect effects (e.g., reduction in insect abundance for prey) caused by negative effects from agricultural land use (i.e., breeding season pesticide application) can affect nestling body condition (Ewald and Aebischer 1999, Brickle et al. 2000, Morris et al. 2005, Hart et al. 2006). Although I was unable to identify clear differences in insect biomass between agricultural and reference sites collected in the passive samplers during the nesting period, terrestrial sweeps conducted in 2013 did indicate clear differences in Diptera abundance between St. Denis and agricultural sites.

Alternatively, nestlings could be ingesting insects which have integrated low levels of pesticides in their tissues. Although insects from Diptera and Odonata are considered the main prey of tree swallows, coleopteran and hemipteran insects have also been identified (McCarty and Winkler 1999a, Johnson and Lombardo 2000, Mengelkoch et al. 2004, Beck et al. 2013). These terrestrial prey are found to be less sensitive to some agricultural pesticides, such as neonicotinoids (Morrissey et al. 2015). Direct transfer of pesticides to tree swallows have been previously documented (Smits et al. 2005, Papp et al. 2007) including detections of neonicotinoids in boluses delivered to nestlings (Haroune et al. 2015). My study only tested for neonicotinoid insecticides in water as a proxy for agrochemical use; however, large differences in their detection and concentration between land types (higher at agricultural sites) suggests

higher agricultural intensity and that other insecticides as well as herbicides and fungicides may represent an added stressor. Concentrations of neonicotinoids detected in the wetlands near the nest boxes were similar to those found in other agricultural wetlands in North America (Morrissey et al. 2015; Smalling et al. 2015) and Europe (Van Dijk et al. 2013) or lower (Anderson et al. 2013). Widespread application of neonicotinoids across the Canadian Prairies (Main et al. 2014) and frequent detections in wetlands across North America and Europe suggest that tree swallows and other aerial insectivore species may be exposed and potentially ingesting insecticides. However, the level of toxicity and effects on nestling body condition need further investigation.

Many factors are associated with lower nestling body condition in tree swallows and other aerial insectivores such as parental quality (Shutler 2006, Harriman 2014), timing of breeding/fledging (Tarof et al. 2011), weather (Dawson 2008) and insect abundance (Ardia 2007). Sites were geographically close and likely had similar weather. After controlling for other factors such as female experience and timing of breeding, lower nestling body condition at agricultural sites remained. Lower mass and condition in nestlings are associated with lower apparent survival in tree swallows (Shutler 2006, Harriman 2014), as well as other avian species (Perrins 1965, Brickhof et al. 1997; Medeiros & Freed 2009). Presence of lower quality nestlings at agricultural sites could contribute to population declines through lower nestling recruitment.

2.4.3 Invertebrate Prey Availability

Numerous studies have found an effect of agriculture on invertebrate biomass (Euliss and Mushet 1999, Wilson et al. 1999, Di Giulio et al. 2001, Benton et al. 2002, Burel et al. 2004, Evans et al. 2007, Rioux Paquette et al. 2013). However, it is evident that variation in invertebrate biomass depends on the sampling method and timing. In my study, agricultural land

use did not negatively influence insect biomass collected from the passive samplers during clutch initiation and egg laying which may explain the lack of an effect on most components of swallow breeding biology. I found that insect abundances collected from terrestrial net sweeps were more consistent with previous work (Thomas and Marshall 1999, Evans et al. 2007) showing lower counts at agricultural sites than at St. Denis. Active insect samplers (i.e., suction traps) identified higher abundances of arthropods in less intensive agricultural landscapes (Benton et al. 2002) and the volume of insects sampled from suction traps and terrestrial sweeps are correlated (Jones 1987). Passive aerial insect samplers have been shown to be effective for within-site comparisons as samplers are placed in the same location and habitat each year. For consistency across sites, passive samplers were placed in open areas on higher ground and away from trees. However, uncontrollable factors such as topography and density of trees and/or wetlands may have created disparities in the distribution and capture rate of insects among sites (Hussell and Quinney 1987). Delettre and Morvan (2000) identified that spatial variation in the richness and abundance of Chironomidae species are affected by hedgerow density and distance to open water. They concluded that insects are sheltered by landscapes with high structural diversity or are filtered into these areas. Thus, placing samplers in open environments may not represent their true availability to swallows because individuals can actively seek insects within the sheltered habitats. Wetland buffer vegetation also acts as a windbreak, inflating aerial insect availability, which translates into higher abundances of aerial insectivores using these habitats for foraging (Whitaker et al. 2000). In my study, agricultural sites tended to be uniformly flat when compared with the reference sites (Michelson, personal observation) and, with the exception of Colonsay in 2012, have fewer trees (Appendix 1), potentially increasing the efficiency of passive samplers through greater wind strength. Wetlands at reference sites had 28% wider shallow marsh zones

and 66% greater treed zones (Anson Main, unpublished data). The greater structural diversity of vegetation at reference sites could reduce spatial dispersal by sheltering aerial insects. Therefore, caution may be needed when interpreting results of inter-site comparisons based on passive samplers. I overcame some of these problems by conducting standardized sweep netting in the same habitat types on each site, with quite different conclusions about site differences.

Alternatively, if the results from the passive samplers are representative of real insect availability then swallows were not food limited in agricultural landscapes which may due to the presence of semi-natural habitats such as grassy ditches and trees. Ditch habitat (grass) and wetlands encompassed ~5% and 5–20%, respectively, of the landscape within the foraging range of swallows and contained greater Diptera abundance than the more available (>50%) upland habitats (grassland or crop). Previous work has found that semi-natural habitats are selectively used for foraging and sustain successful reproduction in a variety of insectivorous bird species (Thomas and Marshall 1999, Whitaker et al. 2000, Girard et al. 2012). Similar to this study, the clutch and brood sizes of corn buntings were unrelated to insect abundance (Brickle et al. 2000). However, buntings were identified to preferentially forage in grassy field margins which accounted for only 1–2% of the available habitat and had insect abundance eight times greater than the non-preferred habitats (Brickle et al. 2000). Therefore, small amounts of semi-natural habitat may harbour sufficient insect prey to maintain the reproductive productivity of swallows.

Although measurements of prey availability across study sites showed inconsistencies, insect abundance from both passive samplers (2012 and 2013 only) and terrestrial sweeps (2013) declined during the nestling period across all habitats in each land type. Late breeding birds may face seasonal impacts of farming practices through seasonal declines in prey. The greater insect abundances initially found in semi-natural habitats decline over time and may not be able to

sustain higher foraging demands later in the season during the chick-rearing period, negatively affecting nestling body condition. Previous studies have reported little or no support that brood size affects nestling growth (De Steven 1980, Zach 1982, Wheelwright 1991, McCarty and Winkler 1999a), yet I found an interaction between clutch initiation date and brood size where body condition of nestlings in larger broods declined faster over the breeding season. Insect abundance declined seasonally as well, suggesting that nestling quality was related to prey availability and — notwithstanding the inconclusive results from the passive samplers — insect abundance may still be lower at agricultural sites during the chick-rearing period.

Disparities about the impacts of cropland landscapes on aerial insects are evident; however, it is clear that nestling body condition is lower at agricultural sites and indirect spatiotemporal variation in Diptera abundance may be an explanation. Further work should be done to determine local habitat effects on insect sampling. However, as previously mentioned, research across North America and Europe has repeatedly found negative effects from agricultural intensification on aerial insect abundance and diversity. Additionally, examining the diet of nestlings may provide insights regarding how agricultural land use affects nestling quality. Land use changes and pesticide application may be altering the local food web by constraining insect diversity and in turn altering the quality of foods available to adult and nestling swallows. Therefore, in Chapter 3, I sampled the diet of adult and nestling swallows, tested for relationships between nestling body condition and diet quality and explored patterns in dietary niche size in adults and nestlings in response to agricultural land use.

CHAPTER 3: SPATIOTEMPORAL VARIATION IN THE DIETS OF ADULT AND NESTLING TREE SWALLOWS: EVIDENCE FROM STABLE ISOTOPE ANALYSES

3.1 INTRODUCTION

Various studies have shown insect abundance and diversity to be lower in landscapes that have been altered from their former natural grassland state to agricultural cropland, where intensive farming practices are employed to increase yields (O'Leaske et al. 1997, Wilson et al. 1999, Vickery et al. 2001). Such agricultural practices focus on shorter crop rotations, reduced crop diversity, increased use of agrochemicals, and removal or degradation of non-farmed habitats such as wetlands and hedgerows (Matson et al. 1997, Stoate et al. 2001, Tscharntke et al. 2005). Despite changes in land-use and food resources, many bird species continue to breed and forage in areas dominated by agriculture, but show a preference towards less intensively cropped areas (Green 1984, Hill 1985, Rodenhouse and Best 1994).

Populations of many aerial insectivorous birds including the swallows, swifts and nightjars have been rapidly declining and a reduction in their main food source, aerial insects, is proposed as a potential causal factor (Smits et al. 2005, Calvert 2012, Smith et al. 2015). At low food availability, birds can forage farther from nests and for longer time periods to compensate (Orians and Pearson 1979), a pattern observed to have direct applications in agricultural landscapes (Brickle et al. 2000). Species within this guild may adjust their foraging time, foraging distance, or prey load size to chicks in response to reductions in food supply (Bryant and Turner 1982). Alternatively, birds may switch their diet in response to changes in the insect community. For example, chimney swifts (*Chaetura pelagica*) included less coleopteran and more hemipteran arthropod prey during periods of high DDT insecticide use (Nocera et al. 2012). The diet of common swifts (*Apus apus*), barn swallows (*Hirundo rustica*), and house

martins (*Delichon urbicum*) in an agricultural habitat tracked temporal changes in prey availability due to natural fluctuations and anthropogenic impacts from farming practices, shifting their diet from oil-seed rape pests to other invertebrate prey groups after the harvest (Orłowski et al. 2014). In swallows (family: *Hirundindae*), preferred prey is chosen when their absolute abundance is high, but swallows will include other prey when the relative abundance of the non-preferred prey is high (Bryant and Turner 1982, Turner 1982b). Thus, diet choice is flexible, even in specialist species such as swallows because of their need to balance foraging costs with energetic gains in space and time. However, individuals that shift to the lower quality but more abundant prey items could have impaired body condition and lower reproductive success (Resano-Mayor et al. 2014). Donald et al. (2001) suggested that shifts in the diet of skylarks (*Alauda arvensis*) were due to increased pesticide applications leading to a reduction in insect diversity which subsequently affected the growth and condition of nestlings.

Here, using stable isotope approaches, I examine variation in insect prey choice and diet diversity of an aerial insectivore species, the tree swallow (*Tachycineta bicolor*), associated with varying levels of agricultural land use. As well, I explore relationships between assimilated diet (i.e., isotopic values of swallow tissue) and adult and nestling body condition. Swallow diets primarily consist of invertebrates of aquatic or terrestrial origin, but in general swallows exhibit a preference for aquatic insects, selecting Diptera (true flies), Ephemeroptera (mayflies) and Odonata (damselflies and dragonflies) over other insect orders commonly associated with terrestrial environments such as Hemiptera (true bugs), Hymenoptera (sawflies, wasps, bees) and Coleoptera (beetles) (Quinney and Ankney 1985, Blancher and McNicol 1988, McCarty and Winkler 1999a). For example, tree swallows select Odonata and Ephemeroptera more often near wetlands and their presence in nestling diets could depend on their availability (Johnson and

Lombardo 2000, Mengelkoch et al. 2004). A high reliance on aerial insects — a pattern common to all aerial insectivores — makes the tree swallow an ideal species for examining potential impacts of agriculture on diet and condition (Calvert 2012).

If abundance of preferred aquatic invertebrates is lower at agricultural sites, relative to reference sites, I hypothesized that swallows will include a larger proportion of prey items not typically found in their diet such as invertebrates of terrestrial origin. As such, the diversity in their diet will be greater which will be represented by a larger isotopic niche width. I also compared the dietary proportions and isotopic niche widths between adults and nestling swallows. The number of insecticide applications is predicted to increase throughout the breeding season, which may cause a seasonal decline in insect abundance. As well, foraging demands are expected to be higher during the nestling period for parents. A potential reduction in prey abundance or seasonal increases in foraging demands from egg laying to the nestling period may result in adults feeding nestlings a greater diversity of aquatic and terrestrial prey than themselves, resulting in larger isotopic niche widths. Finally, I also explored relationships between the diet (represented by tissue stable isotope values) of adult and nestling swallows and their respective body condition. If tree swallows are consuming less preferred prey at agricultural sites or later in the breeding season (i.e., during the nestling period), then body condition may be lower. Alternatively, swallows may select for preferred prey items, but due to predicted lower abundances at agricultural sites or a decline in abundance later in the season, swallow body condition may also be lower. Understanding how birds adapt to changes in food abundance and diversity due to agricultural land use could offer insights into the mechanisms that produce lower reproductive success or lower body condition.

3.2 METHODS

3.2.1 Tree Swallow Study Sites

I monitored breeding tree swallows on 4 main study sites (Burr, Colonsay, Humboldt and St. Denis) in 2012 and 2013. See Chapter 1 for full site descriptions and nest box monitoring methods of swallows. Characterization of the land use around the boxes using orthophoto imagery and GIS mapping distinguished Burr, Colonsay 2012, Colonsay 2013, and Humboldt as agricultural sites and St. Denis is a reference site containing mostly pasture and grasslands. See Chapter 2 for full analysis details and justification for grouping two sub-sites at Colonsay as one site.

3.2.2 Field Sampling

3.2.2.1 Insect Prey Collections from Terrestrial Net Sweeps

Standardized net sweeps were completed to sample a wide variety of terrestrial and emergent aquatic insect orders in the vicinity of nest boxes. In 2012, I sampled insects by sweeping the vegetation at various heights in the ditches and upland/cropped area with a 15 cm diameter butterfly net. I completed approximately 100 sweeps per transect at three locations near the line of tree swallow nest boxes. Sampling was repeated three times at approximately 10 day intervals starting on 23 June, which corresponds with peak hatching of nestling swallows in that year.

Standardized sweeps were more comprehensive in 2013 to include three time periods (peak incubation, peak hatch, and 12 days post-hatch) in three main habitats 1) upland (cropland or grassland); 2) along the nest box line in the dry ditch (hereafter, ditch) and; 3) in wetland

vegetation (wet meadow and emergent wetland zones). Open cropland and grassland areas were classified as one habitat type because individual sites had only one or the other type near the nest boxes which precluded a comparison among sites. Swallows are routinely observed feeding in these habitats and over water bodies (McCarty and Winkler 1999a, Michelson, personal observation), and so were assumed to provide a representative sample of the full insect community potentially available to swallows. To maintain standardization among habitats and sites, each 75 m transect was swept 150 times, at various heights within the vegetation, with a 15 cm diameter butterfly net. Each transect was completed within 3–4 minutes. Although the number of new species of insects in a net sweep sample typically plateaus after ~60 sweeps (Davis and Gray 1966), I increased the number of sweeps per transect to obtain sufficient sample mass of each insect order for stable isotope analysis. All transect sweeps were conducted into the wind at wind speeds < 25 km/hr. All sweeps were completed when minimum temperature exceeded 18.4˚C, i.e., when aerial insects are expected to be more active (Winkler et al. 2013). Insects were collected from 4–29 June in 2013.

Insects were counted and identified to order (Triplehorn and Johnson 2005). In addition, due to the importance of Diptera to the diet of tree swallows and potential negative effects on their abundance from agricultural practices, Diptera were further classified as aquatic/semi-aquatic (i.e., Chironomidae and Culicidae) and terrestrial (all other dipterans). Tipulidae prey (order: Diptera), although rare (<5 individuals), were included with aquatic Diptera in 2012 but were not in 2013 since these latter samples were much larger than the size of prey typically eaten by tree swallows and other aerial insectivores (McCarty and Winkler 1999a, Beck et al. 2013).

3.2.2.2 Tree Swallow Sampling

Adults were captured when their nestlings hatched and were banded and measured for lengths of the wing and 9th primary feather (nearest 0.5 mm with a wing-ruler), head-bill length (nearest 0.01 mm with calipers), and body mass (nearest 0.5 g with a Pesola scale). At 12 days post-hatch, nestlings were banded and measurements (same as adults) were recorded. Blood samples were collected from adults at hatch and from nestlings at 12 days post-hatch. Blood was taken by venipuncture of the brachial wing vein, collected in heparinized capillary tubes and stored on ice. Samples were centrifuged at the end of the day for 10 min at 8000 rpm to isolate red blood cells which were stored in micro-centrifuge tubes at -80 ˚C. Stable isotope values of red blood cells are known to reflect the integrated isotopic diet of birds over 2–3 weeks (Hobson and Clark 1993, Boecklen et al. 2011). Three nestlings were sampled per nest box and red blood cells were pooled to obtain sufficient sample volume for stable isotope analysis. Blood was sampled from nestlings at 62 and 83 nests and from 113 and 160 adults in 2012 and 2013, respectively. In 2012, adults were sampled from 11 June to 13 July and nestlings from 19 June to 23 July. In 2013, sampling dates were 10 June to 16 July for adults and 21 June to 29 July for nestling swallows.

3.2.3 Stable Isotope Analysis

Insects and red blood cells of swallows were freeze dried for a minimum of 24 hours until dry. The insects were then ground to a powder using a mortar and pestle. Approximately 1 mg dry mass was weighed into a tin capsule prior to stable isotope analysis. Insects collected in 2012 were analyzed at the Stable Isotope Facility at the University of Saskatchewan using a Delta V isotope ratio mass spectrometer and Conflo IV interface (Thermo Scientific, Bermen, Germany), coupled to a Costech ECS4010 elemental analyzer (Ventura, California) using a PN150 autosampler. Red blood cell samples from both years and insect samples collected in 2013 were

analyzed at the Stable Isotope Facility at University of California, Davis, using a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) with a PDZ Europa ANCA-GSL elemental analyzer. In 2012, lab references were calibrated against NIST Standard Reference Materials IAEA-N1 and IAEA-N2 with a measurement accuracy of ± 0.05‰ (δ^{13}C) and ± 0.27‰, (δ^{15}N). Precision between duplicate lab reference samples was ± 0.02‰ (δ^{13}C) and ± 0.07‰ (δ^{15}N). Measurement accuracy of lab references in 2013 was ≤ ± 0.28‰ and ≤ ± 0.49‰ for δ^{13}C and δ^{15}N, respectively, and were calibrated against NIST Standard Reference Materials IAEA–N1, IAEA–N2, IAEA–N3, USGS–40, and USGS–41. Duplicates samples of reference material had a precision ≤ ± 0.08‰ and ≤ ± 0.19‰ for δ^{13}C and δ^{15}N, respectively. Isotopic compositions of ^{13}C and ^{15}N are expressed relative to VPDB (Vienna Pee Dee Belemnite; ^{13}C) and air (^{15}N) in delta (δ) notation as parts per mil (‰).

3.2.4 Statistical Analysis

3.2.4.1 Mixing Models to assess Tree Swallow Diet

Bayesian stable isotope mixing models were performed in MixSIAR GUI (graphical user interface) in R (R Core Team 2013) to identify the proportional contribution of insect sources in the diet of adult and nestling tree swallows (Moore and Semmens 2008, Stock and Semmens 2013). This package allows the inclusion of a fixed effect, such as study site, which examines the diet of swallows among sites while using separate site-specific dietary sources (Semmens et al. 2009). Therefore, the mean ± standard deviation of values of δ^{13}C and δ^{15}N for different insect taxa from each site were included as prey sources in the mixing models. Insect δ^{13}C and δ^{15}N values changed subtly for both isotopes (< 0.6 ‰) between sampling periods in 2013. To account for this small variation, insects sampled during incubation and hatch were used as sources for

adult diets while insects sampled during hatch and the nestling period were used as sources for nestlings. In 2012, some $\delta^{13}C$ values of adult swallows were more negative than the prey sources and may be attributed to some swallows being sampled before insects. These Bayesian mixing models incorporate error to account for uncertainty providing a robust analysis of diet.

The isotopic signatures of Coleoptera, Hemiptera, Hymenoptera, Lepidoptera and Orthoptera were grouped by site and year as "Terrestrial Orders" *a priori* as these orders showed substantial overlap in their isotopic signatures (Appendices 5 & 6) and represent a small proportion of the diet (Mengelkoch et al. 2004, Beck et al. 2013). Similarly, Odonata and aquatic Diptera samples were grouped as an "Aquatic Orders" signature *a posterior* because mixing models could not distinguish between the two sources (Appendices 5 & 6). "Terrestrial Diptera" were retained as a separate group as they did not overlap with the other prey sources and were central to the prediction that tree swallows may show differential selectivity for Diptera across agricultural and reference site types (McCarty and Winkler 1999a). Tricoptera isotope values were distinct but were excluded from the mixing models because, if present at a site, there was only one sample, eliminating the ability to incorporate variation in the isotope values, a requirement for mixing models in MixSIAR (Phillips et al. 2014).

A diet-tissue trophic enrichment factor (TEF) is incorporated in the mixing models to account for changes in the isotopic ratio between the food source and the consumer (Hobson and Clark 1992). TEFs of 1.74 ± 0.26‰ and 2.48 ± 0.44‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, were used in this study which are the mean and standard deviation of TEFs found for red blood cells in three separate captive diet-switching experiments for species which are primarily insectivorous in the breeding season (Hobson and Bairein 2003, Pearson et al. 2003, Evans Ogden et al. 2004). Values were not corrected for lipids because C:N ratio in red blood cells was anticipated to be

low. Separate mixing models were completed for 2012 and 2013 and for adults and nestlings within each year, as the isotopic values of tree swallows and insects were different between years (Appendices 5 & 6).

General linear models (glm, package *stats*, R version 3.1.3) were used to test differences in the source proportions between sites and swallow age classes (as previously used by Inger et al. (2006) and Resano-Mayor et al. (2014)). The posterior distributions of the mixing model dietary estimates were used as the response variable while site, age class (adult or nestling) and their interaction were explanatory variables. Separate models were run for each prey source and year (six models). Proportions were arcsine square-root transformed prior to analysis to improve normality. *Post-hoc* Tukey tests were used to compare proportions of a prey source for adults and nestlings among sites as well as comparisons between adults and nestlings within a site while controlling for interaction effects (lsmeans, package *lsmeans*, R version 3.1.3).

3.2.4.2 Isotopic Niche Width

To further examine effects of agricultural land use on the diet of swallows I examined the isotopic niche width of adults and nestlings at each site in 2012 and 2013 using the Bayesian standard ellipse area (SEA.B) metric in the Stable Isotope Bayesian Ellipses package in R (SIBER; Jackson et al. 2011). Stable isotope values (δ^{13}C and δ^{15}N) of swallow red blood cells were used as x and y coordinates to define the shape and size of the isotopic niche space of a population (i.e., adults at site Burr). Unlike the traditional metrics such as the convex hull, ellipses are unbiased with respect to sample size and are more robust as Bayesian techniques are ideal for comparing groups with different sample sizes. A posterior distribution of 10,000 iterations per age class, site, and year was produced. To examine differences in the isotopic niche

widths among age classes and sites, general linear models were used with site, age, and their interaction as explanatory variables (glm, package *stats*, R version 3.1.3; years tested separately). The response variable, SEA.B, was log-transformed prior to analysis to improve normality. *Post-hoc* Tukey contrasts were used to compare adult and nestling isotopic niche sizes between study sites in each year as well as between age classes within each site (lsmeans, package *lsmeans*, R version 3.1.3).

3.2.4.3 Relationships between Assimilated Diet and Swallow Body Condition

Relationships between adult and nestling condition with their assimilated diet, represented by their stable isotope values, were tested. I used three body measurement responses (mass, size, and body condition) to examine effect of diet on adult and nestling condition. The assimilated diet of adults encompasses their diet from 2-3 weeks prior to hatch while nestling stable isotope values represent their assimilated diet from hatch to 12 days old when they are measured and sampled for blood.

An index of size of swallows was developed by completing a principal component analysis (PCA; prcomp, R version 3.1.3) of the three structural measurements (wing, 9^{th} primary feather, and headbill lengths) for adults and nestlings, separately. PC1 accounted for 67% and 85% of the variation in the structural measurements of adults and nestlings, respectively. A body condition index (BCI) was produced by using the residuals of mass regressed against PC1. Indices for adults and nestlings were developed separately.

To examine relationships between the assimilated diet (i.e. stable isotope values) with body measurement and condition of adult and nestling swallows, linear mixed effects models (lmer, package *lme4*, R version 3.1.0) were used. Adult mass, structural size (PC1) and BCI were

tested with land type (land), sex, swallow δ^{13}C and δ^{15}N values, and their interactions as fixed effects. Random effects included date, nest box type, and site (nested in year). Similarly, nestling mass, PC1 and BCI were evaluated against land type, values of δ^{13}C and δ^{15}N, and interactions as fixed effects while nestling age, nest box type and date (nested in year) were included as random effects. To account for seasonal and site differences in the stable isotope values of the food web, I adjusted the swallow isotope values by baseline insect stable isotope values at their respective sites. Adult values were adjusted by δ^{13}C values of Odonata in 2012 and aquatic Diptera in 2013 and δ^{15}N values of Orthoptera in both years. Nestling values were adjusted by baseline values of Odonata in 2012 for δ^{13}C and Orthoptera for δ^{15}N in both years. Red blood cells from the three nestlings sampled per nest box were physically pooled prior to freeze drying and stable isotope analysis. As such, the mean of the body measurement response variables for the three nestlings sampled for blood per nest box was taken; thus, the unit of measure is nest box identification for nestlings. Adults were not pooled by nest box and analyzed as individuals. An intercept-only model (statistical null) was included in candidate model sets. Information-theoretic approaches (Akaike's Information Criterion for small sample sizes, AIC_c; Burnham and Anderson 2002) were used for model selection to determine relative support for a variable's inclusion. The top models were run using restricted maximum likelihood estimation procedures to obtain parameter estimates (± S.E.)

3.3 RESULTS

The "Aquatic Orders" prey source had consistently lower δ^{13}C values than both terrestrial prey sources and had similar δ^{15}N values to "Terrestrial Diptera" (Figure 3.1). Large variation

existed within the “Terrestrial Orders” group, attributed to the wide variety of insect orders included in this source.

The stable carbon isotope values of swallows ranged from -29.45‰ to -25.40‰ for adults and -29.55‰ to -24.39‰ for nestlings while their stable nitrogen isotope values ranged from 9.56‰ to 14.45‰ and 9.60‰ to 13.92‰, respectively (Figure 3.1). Swallows at one agricultural site, Humboldt, had much higher δ^{15}N values than the other sites which may be due to site-specific differences in farming practices such as nitrogenous fertilizer inputs or local water and soil properties (Heaton 1986, Kendell et al. 1995, Harrington et al. 1998, Kendell 1998, Hebert and Wassenaar 2001, Anderson and Cabana 2005). A paired t-test comparing stable isotope values of the blood of adults to chicks from the same nest box did show a significant difference in values of δ^{13}C ($t = -15.75$, $df = 145$, $p < 0.001$); however, the difference between the means was small (1.00 ± 0.06‰). Red blood cells of adults and nestlings also showed a small but significant difference in values of δ^{15}N ($t = 3.08$, $df = 145$, $p = 0.002$) where the mean values of the nestlings were 0.14 ± 0.04‰ higher than their parents. Natural temporal shifts in the isotopic values of the prey, age-related differences in trophic enrichment factors (Kurle et al. 2013) and metabolic rates in growing chicks (Sears et al. 2009) may be driving small differences between age classes.

3.3.1 Dietary Patterns

On average, approximately 75% of the adult and nestling swallow diet was “Aquatic Orders” across all study sites and years (Figure 3.2). Contrary to my prediction, in 2012 swallows at the St. Denis reference site foraged less on “Aquatic Orders” (median: 55–81%) and ate a higher proportion of “Terrestrial Diptera” (14–38%) than swallows at agricultural sites

("Aquatic Orders": 69–97%; "Terrestrial Diptera": 1–38%); however, this relationship was not seen in 2013 (Appendix 8). Adults at the agricultural site, Colonsay, showed the largest

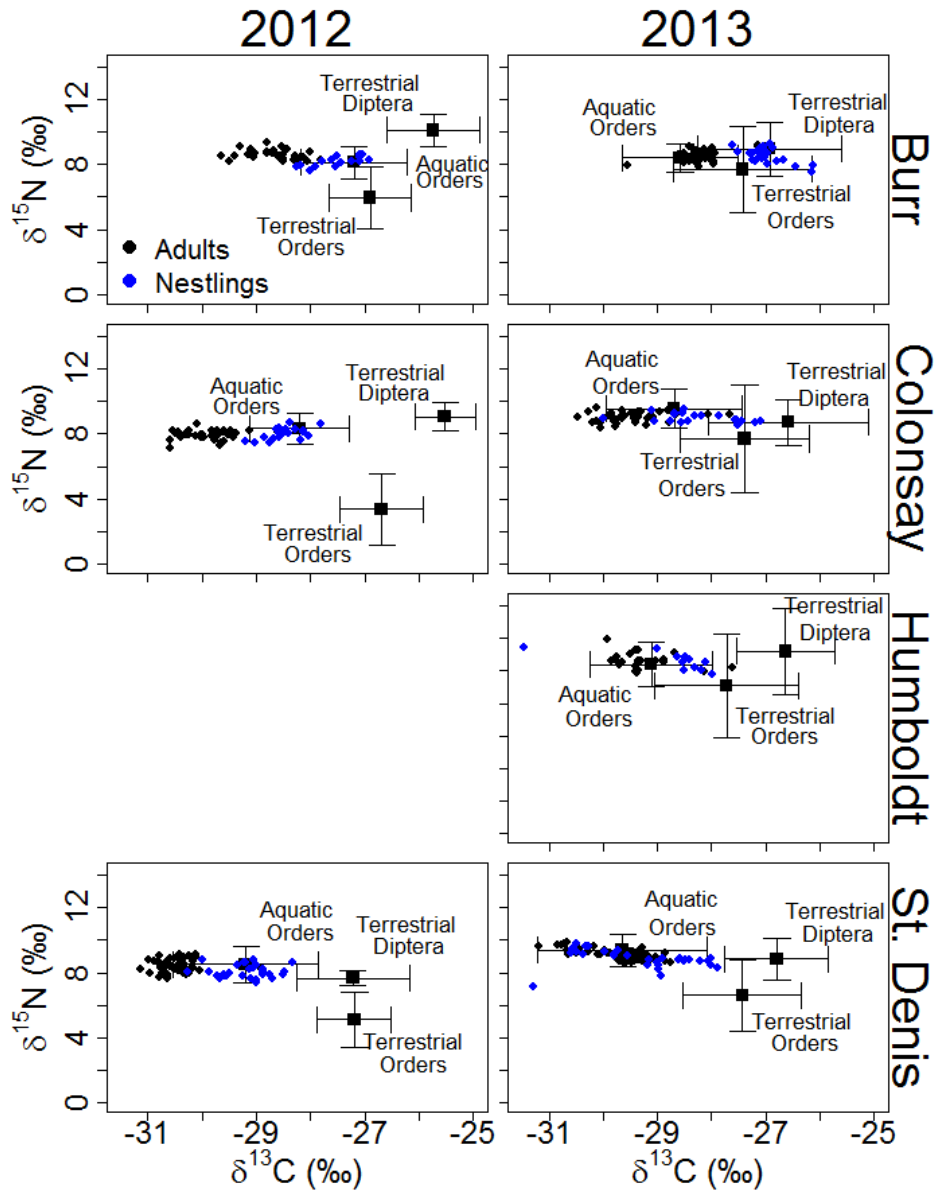

Figure 3.1. Biplot of mean ± S.D. of $\delta^{13}C$ and $\delta^{15}N$ of prey sources (black squares) and tree swallow adults (black circles) and nestlings (blue circles) sampled at three agricultural sites (Burr, Colonsay, Humboldt) and one reference site (St. Denis) in 2012 (left) and 2013 (right). Swallow stable isotope values were TEF adjusted by 1.74 ± 0.26 ‰ and 2.48 ± 0.44 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Refer to Appendices 5 and 6 for sample sizes, raw isotope values and C:N ratios.

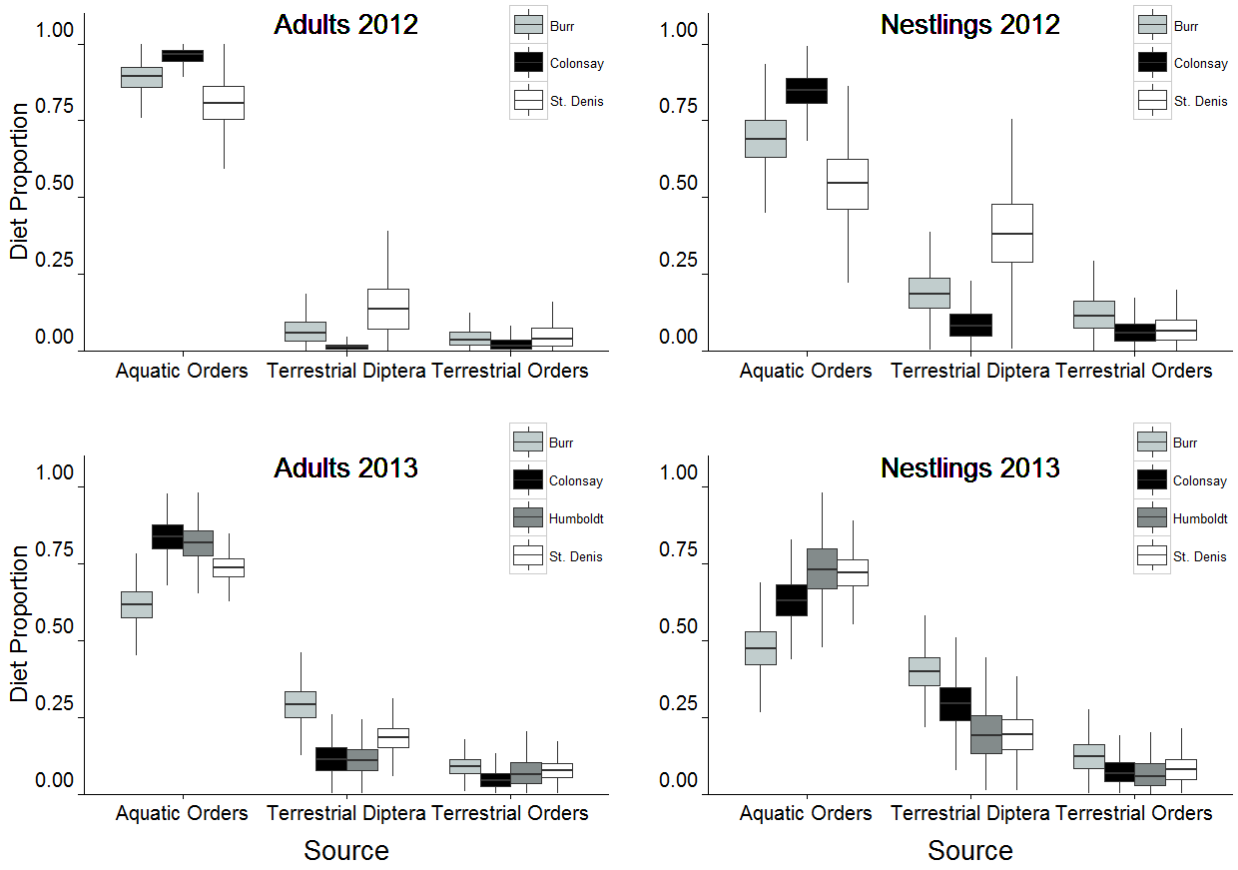

Figure 3.2. Proportions of three prey source groups in the diets of adult and nestling tree swallows in 2012 (top panels) and 2013 (bottom panels). Agricultural sites are in light grey (Burr), black (Colonsay) and dark grey (Humboldt) and the reference site is white (St. Denis). The line in the boxplot is the median proportion of diet sources. The bottom and top of the boxes represent the 25% and 75% credible intervals, respectively, and error bars are the 95% credible intervals calculated in a Bayesian mixing model of tree swallow blood samples relative to site-specific isotopic signatures of the three prey sources. "Aquatic Orders" include aquatic insect families in the orders Diptera and Odonata while "Terrestrial Orders" include insects from the orders Coleoptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera. Sample sizes include 115 and 162 adults in 2012 and 2013, and 63 and 85 nest boxes in 2012 and 2013, respectively.

proportions of "Aquatic Orders" in 2013 (84%), followed Humboldt (82%; agricultural), St. Denis (74%; reference), and then Burr (62%; agricultural), while in nestlings the sequence from highest proportion of "Aquatic Orders" to lowest was Humboldt (73%), St. Denis (72%),

Colonsay (63%), and then Burr (47%). *Post-hoc* Turkey comparisons found significant differences ($p < 0.01$) in the proportion of each prey source between sites (Appendix 7). Exceptions included the similar proportions of "Terrestrial Diptera" between adults from Colonsay and Humboldt ($\beta = 0.01 \pm 0.002$, $p = 0.20$) and between nestlings from Humboldt and St. Denis in 2013 ($\beta = 0.002 \pm 0.002$, $p = 0.97$; Appendix 7). Annual variation was greater than site specific patterns in the diet, such that there was no clear difference between swallows at agricultural sites than those nesting at St. Denis. Across all sites and in both years there appears to be a trade-off between the proportion of insects from "Aquatic Orders" in the swallow diet and "Terrestrial Diptera". While "Aquatic Orders" were clearly the majority of the diet at all sites and years, birds with a lower proportion of insects from "Aquatic Orders" in the diet corresponds with an increase in "Terrestrial Diptera" and vice versa, and the degree varies from year to year.

The diets of both adult and nestling swallows consisted mainly of insects from "Aquatic Order" and "Terrestrial Diptera" (median range 87–98% of diet; Figure 3.2). Detailed estimates of dietary proportions from the mixing models by year, site, and age group revealed that adults had a higher proportion of "Aquatic Orders" in their diet (62–97%) while nestlings had included higher proportions of "Terrestrial Diptera" and "Terrestrial Orders" (14–52%; Appendix 8). Diets were different between adults and nestlings for all sources across all sites and years (Table 3.1), with the following exceptions: the proportions of "Terrestrial Orders" were similar between adults and nestlings at Humboldt and St. Denis in 2013. Mean difference in the median diet proportion of prey sources between adults and nestlings across all sites and years was 15% for "Aquatic Orders", 12% for "Terrestrial Diptera", and 3% for "Terrestrial Orders".

Table 3.1. Estimates (± S.E.) of *post-hoc* Tukey contrasts comparing the Bayesian posterior distributions of the source proportions for adults versus nestlings within the same study site. Positive values indicate the adults have a larger proportion of the prey source than nestlings. All comparisons were significant ($p < 0.001$) with the exception for those bolded.

Year	Site	Aquatic Orders	Terrestrial Diptera	Terrestrial Orders
2012	Burr	0.26 ± 0.002	- 0.20 ± 0.003	- 0.14 ± 0.002
	Colonsay	0.20 ± 0.002	- 0.18 ± 0.003	- 0.20 ± 0.002
	St. Denis	0.30 ± 0.002	- 0.30 ± 0.003	- 0.05 ± 0.002
2013	Burr	0.14 ± 0.002	- 0.11 ± 0.002	- 0.05 ± 0.002
	Colonsay	0.24 ± 0.002	- 0.23 ± 0.002	- 0.05 ± 0.002
	Humboldt	0.10 ± 0.002	- 0.12 ± 0.002	**0.01 ± 0.002**
	St. Denis	0.02 ± 0.002	- 0.01 ± 0.002	**- 0.004 ± 0.002**

3.3.2 Comparing Isotopic Niche Widths

Isotopic niches widths were significantly different between study sites (from *post-hoc* Tukey tests all $p < 0.001$) with larger site differences in 2013 than 2012 (Figure 3.3, Appendix 9). In 2012, adults at Burr had a larger isotopic niche (agriculture; β = -0.42, S.E. = 0.002) than St. Denis (reference; β = -0.49, S.E. = 0.002) and Colonsay (agriculture; β = -0.50, S.E. = 0.002; Figure 3.3). Nestlings also showed the same pattern where the isotopic niche of Burr was larger (β = -0.20, S.E. = 0.002) than St. Denis (β = -0.24, S.E. = 0.002) and Colonsay (β = -0.41, S.E. = 0.002). However, in 2013, the pattern was different. Burr (agricultural) had the smallest isotopic niches for both adults (β = -0.81 ± 0.002) and nestlings (β = -0.38, S.E. = 0.002) and the agricultural site, Humboldt had the largest niche width (Adults: β = 0.14, S.E. = 0.002; Nestlings: β = 0.60, S.E. = 0.002; Figure 3.3). Adults at Colonsay had larger isotopic niches (β = -0.32, S.E. = 0.002) than St. Denis (β = -0.59, S.E. = 0.002) but for nestlings, the relationship was reversed such that niche widths at Colonsay (β = 0.03, S.E. = 0.002) were smaller than St. Denis (β =

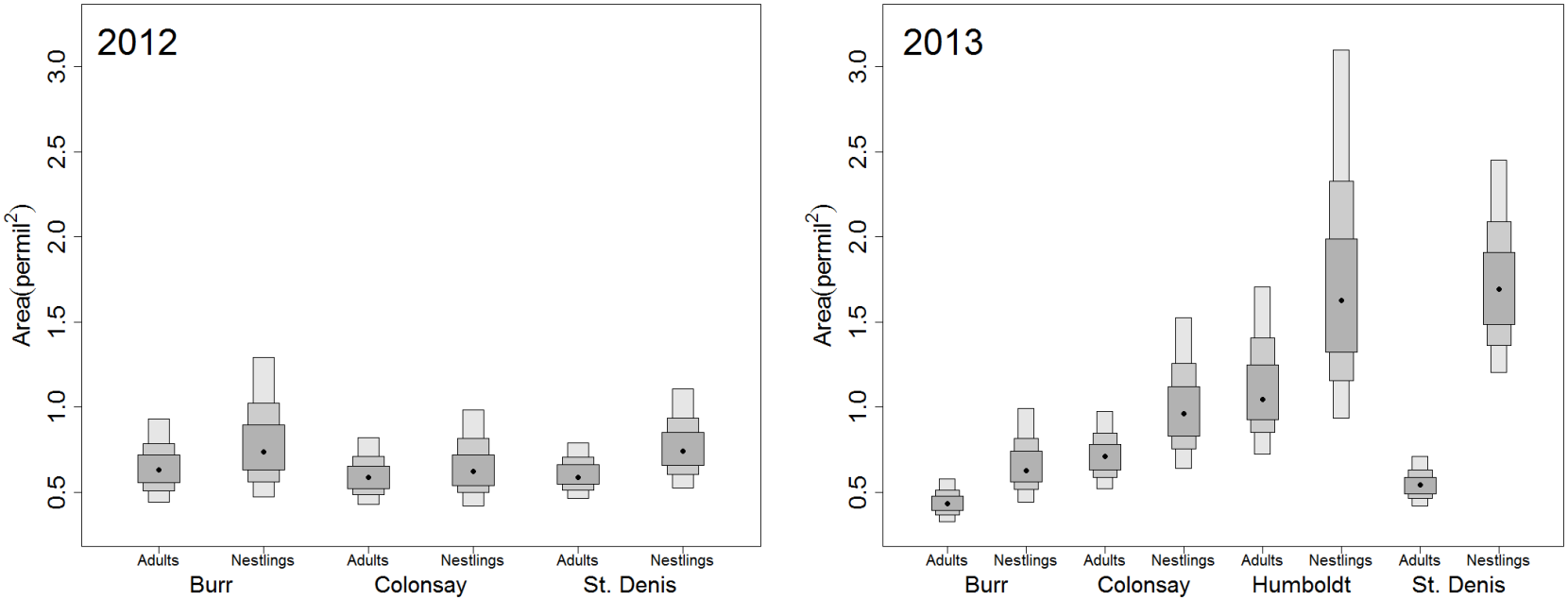

Figure 3.3. Bayesian estimated ellipse areas (permil^2) for adults and nestlings tree swallows in 2012 (left) and 2013 (right). The central dot is the median value of the estimates and the 50%, 75%, and 95% credible intervals are in dark grey, medium grey, and light grey boxes, respectively. Sample sizes include 115 and 162 adults in 2012 and 2013, and 63 and 85 nest boxes in 2012 and 2013, respectively.

Table 3.2. Difference (Estimate), standard error (S.E.) and Z scores, of *post-hoc* Tukey contrasts comparing the isotopic niche widths of adults versus nestlings within the same study site. Nestlings had larger isotopic niches than adults (negative values) at all sites and in both study years. All tests had a p-value < 0.001.

Year	Nestlings	Estimate	S.E.	Z Score
2012	Burr	-0.22	0.003	-78.93
	Colonsay	-0.09	0.003	-33.92
	St. Denis	-0.24	0.003	-88.51
2013	Burr	-0.43	0.003	-152.57
	Colonsay	-0.35	0.003	-124.00
	Humboldt	-0.45	0.003	-160.87
	St. Denis	-1.16	0.003	-410.86

0.57, S.E. = 0.002). Therefore, I could not find a clear, consistent distinction in the isotopic niche widths between agricultural sites and the reference site at St. Denis (Appendix 9).

As predicted, nestlings had larger isotopic niche widths than adults from the same site (all $p < 0.001$; Figure 3.3, Table 3.2). The differences in the niche widths between adults and nestlings were greatest at the reference site, St. Denis, particularly in 2013.

3.3.3 Assimilated Diet and Body Condition

Adult swallows at the reference site, St. Denis, had higher body mass ($\beta = 0.74 \pm 0.36$) and body condition index ($\beta = 0.68 \pm 0.33$) than swallows at the agricultural sites (Table 3.3; Appendix 10). Male swallows had a slightly lower mass ($\beta = 0.26 \pm 0.13$) but larger structural size ($\beta = 1.58 \pm 0.14$) than females, resulting in lower body condition than females ($\beta = 0.46 \pm 0.13$). Stable isotope values ($\delta^{13}C$ or $\delta^{15}N$) of red blood cells was not a significant variable explaining variation in adult body

measurements and condition suggesting that diet during the pre-hatching period does not significantly influence breeding condition.

Blood stable isotopes of the nestlings also suggested diet was not a strong predictor of mass, size or body condition. Land use type or the null model were the best supported models. Nestlings at the reference site, St. Denis, were slightly heavier ($\beta = 0.61 \pm 0.40$) and smaller ($\beta = 0.26 \pm 0.20$) than those at agricultural sites, and nestlings at St. Denis had higher body condition than those at agricultural sites ($\beta = 0.66 \pm 0.35$; Table 3.4; Appendix 10). Although the $\delta^{13}C$ variable was present in some of the top models explaining nestling mass and body condition, model weight and effect sizes were low. The relationship between $\delta^{13}C$ and mass was not significant ($\beta = -0.17 \pm 0.16$, $p = 0.32$). Parameter estimates for the second-ranked model explaining nestling BCI (land + $\delta^{13}C$) also showed higher condition in nestlings at St. Denis relative to agricultural sites ($\beta = 0.75 \pm 0.34$) as well as a weak positive relationship with values of $\delta^{13}C$ ($\beta = 0.09 \pm 0.13$, $p = 0.50$).

Table 3.3. Model selection results testing relationships between the isotopic values of adult red blood cells to mass, structural size (PC 1), and body condition index (BCI) using mixed effects models. Fixed effects included land type, sex, $\delta^{13}C$, $\delta^{15}N$ and their interactions. Site nested in year, box type and date were included as random effects. Adults were analyzed as individuals (n=273). Only models with $\Delta AIC_c < 2$ and the intercept-only model (null) are presented.

Response	Model Structure	K[1]	AIC_c[2]	ΔAIC_c[3]	Deviance[4]	w_i[5]
Mass	land + sex	8	849.25	0.00	832.70	0.13
	land + sex + land × sex	9	849.92	0.68	831.24	0.09
	land + sex + $\delta^{15}N$	9	850.56	1.31	831.88	0.07
	land	7	850.87	1.62	836.44	0.06
PC 1	sex	7	862.69	0.00	848.28	0.18
	land + sex	8	862.96	0.27	846.42	0.16
	sex + $\delta^{15}N$	8	864.67	1.97	848.12	0.07
	land + sex + land × sex	9	864.69	1.99	846.00	0.07
BCI	land + sex	8	837.26	0.00	820.72	0.17
	land + sex + land × sex	9	837.61	0.36	818.92	0.14
	land + sex + $\delta^{15}N$	9	838.69	1.44	820.02	0.08
	land + sex + $\delta^{15}N$ + land × sex	10	839.11	1.85	818.28	0.07
	sex	7	839.22	1.97	824.80	0.06

[1] Number of estimable parameters.
[2] Akaike's Information Criterion for small sample sizes.
[3] Difference in AIC_c between each model and the model with the lowest AIC_c value.
[4] -2 × log likelihood.
[5] Model weight.

Table 3.4. Model selection results testing relationships between isotopic values of nestling red blood cells (n = 145 nestling pools) to mass, structural size (PC 1), and body condition index (BCI) using mixed effects models. Fixed effects included land type, box type, $\delta^{13}C$, $\delta^{15}N$ and their interactions. Date, box type and site (nested in year) were used as random effects. Responses were the mean of the three chicks sampled for blood in each nest box. Only models with $\Delta AIC_c < 2$ and the intercept-only model (null) are presented.

Response	Model Structure	K[1]	AIC_c[2]	ΔAIC_c[3]	Deviance[4]	w_i[5]
Mass	land	8	544.07	0.00	527.00	0.22
	null	7	544.20	0.13	529.38	0.20
	$\delta^{13}C$	8	545.74	1.68	528.68	0.09
	land + $\delta^{15}N$	9	545.78	1.71	526.44	0.09
PC 1	null	7	489.43	0.00	474.62	0.29
	land	8	490.05	0.62	473.00	0.21
BCI	land	8	519.86	0.00	502.80	0.21
	land + $\delta^{13}C$	9	521.15	1.29	501.82	0.11
	null	7	521.18	1.32	506.36	0.11
	land + $\delta^{13}C$ + land × $\delta^{13}C$	10	521.25	1.39	499.62	0.10
	land + $\delta^{15}N$	9	521.34	1.48	502.00	0.10

[1] Number of estimable parameters.
[2] Akaike's Information Criterion for small sample sizes.
[3] Difference in AIC_c between each model and the model with the lowest AIC_c value.
[4] -2 × log likelihood.
[5] Model weight.

3.4 DISCUSSION

I examined the isotopic diet of tree swallows on study sites with varying levels of agricultural land use. At all sites, the majority of the diet of swallows was comprised of insects

from “Aquatic Orders”, with much lower reliance on “Terrestrial Diptera” and “Terrestrial Orders”. Insects from “Terrestrial Orders” made up a very small proportion of the diet overall and a trade-off existed in the proportion of “Aquatic Orders” and “Terrestrial Diptera” where the higher the proportion of one source resulted in a lower proportion of the other. Nestlings consistently had a more diverse diet than adults, incorporating a larger proportion of “Terrestrial Diptera” and larger overall niche widths. Proportions of each prey source varied across all sites for both adults and nestlings in 2012 and 2013. Similarly, differences in isotopic niche widths between sites and age classes were found but the high variation limited my ability to detect any clear distinction between agricultural sites and the reference site at St. Denis. Sites where swallows consumed a high proportion of insects from “Aquatic Orders” in their diet had large niche widths while sites where swallows consumed similar proportions of “Aquatic Orders” and “Terrestrial Diptera” had smaller niche widths. No relationships were evident between assimilated diet and body condition measures in either age group.

3.4.1 Site-related Diet Differences

Proportions of aquatic and terrestrial prey sources in the swallow diet were highly variable among sites and years despite the differences in agricultural land use. This emphasizes the complexity of modelling bird population responses at the site level, where local and seasonal effects may mask effects of land use. In Chapter 2, I was unable to detect a site-level effect of agricultural land use on insect biomass and abundance throughout the breeding season. Small patches of semi-natural habitat such as road side ditches with grass and perennials, trees and shrubs, and wetlands may provide adequate abundances of insects even in cropland dominated areas. However, the insect community could be influenced by slightly different agricultural practices that are not consistent among the agricultural sites. Grüebler et al. (2008) found that

during periods of low abundances of flying insects, the highest densities of remaining insects were found in highly structural habitats such as hedgerows and trees while abundances of flying insects were low in habitats such as agricultural fields and meadows, particularly during cold and windy weather. Several studies have reported higher species richness for above-ground insects, including flying insects, in semi-natural areas surrounded by agricultural fields (Duelli et al. 1999, Thomas and Marshall 1999, Grüebler et al. 2008). St. Denis has good quality terrestrial habitat dominated by native and non-native grasses and trees, while the agricultural sites are dominated by cropland and grassy ditches with some trees. The larger proportion of natural terrestrial habitat at St. Denis may increase the availability of terrestrial insects resulting in tree swallows at this site to forage on this highly available source. This could help to explain why, in 2012, swallows at St Denis had higher proportions of "Terrestrial Diptera" in their diets. Beck et al. (2013) found similar patterns where swallows closer to sites contaminated by trace elements consumed aquatic prey sources, while swallows further downstream at more pristine sites consumed a terrestrial-based diet. They attributed this difference to higher abundances of terrestrial insects at uncontaminated sites. At contaminated sites, grasses were mowed, leaving the aquatic stream habitat as the only productive source for insect prey. Variation in diet proportions among agricultural sites could also be due to changes in the insect communities between sites each year and site differences in wetland abundances and permanency (Williams 1996), nutrient additions (Matthaei et al. 2010, Mantyka-Pringle et al. 2014) and pesticide applications (Kragen et al. 2011, Van Dijk et al. 2013). Seasonal agricultural practices — such as timing of seeding, pesticide applications, tillage and mowing — change with crop type and year and may be more important in determining prey availability. Thus, subtle site-specific patterns in

the diet may be attributed management practices causing differences in insect refuges that vary with year to year agricultural planning.

There was no strong distinction between agricultural sites and St. Denis in terms of the isotopic niche widths of swallows. Populations with individuals that forage on similar prey will have a small isotopic niche (Matthews and Mazumder 2004), but populations with individuals that have highly specialized individual diets and large variation among individuals will have large isotopic niche widths (Bolnick et al. 2007). This pattern was observed in this study as a site where individual swallows had a more generalist diet (i.e., similar proportions of "Aquatic Orders" and "Terrestrial Diptera") formed a population of swallows with a small isotopic niche. Conversely, sites such as Humboldt and St. Denis in 2013 had a population of swallows that foraged largely on one prey group ("Aquatic Orders") but had large isotopic niches. This may be a result of among individual variation in foraging habitats, greater prey species richness or some individuals eating different prey than the majority of the population. Evolutionary theories support the idea that a population with large niche widths is composed of individuals which specialize in a local area or on a particular prey type (Roughgarden 1972). As well, if resources are high, it is advantageous for individuals to specialize on prey not used by conspecifics rather than trying to compete (Krebs et al. 1977). Alternatively, when overall prey abundance is low at a site, individual swallows may be forced to forage on similar prey resulting in high individual niche overlap and small population niche width — such as the case of all groups in 2012 and adults at Burr and St. Denis in 2013. But when prey abundance is high, individual swallows may specialize on different prey or on the same prey from differing habitats with distinct isotopic signatures, resulting in little individual niche overlap and a large population-level niche width — such as in adults and nestlings at Humboldt in 2013 and in nestlings at St. Denis in 2013. Further

studies should follow up with temporal tissue sampling to examine variation within and among individuals of a population (Matich et al. 2011) to help decipher variation due to the prey or due to individual swallow foraging strategies. This study displays interesting patterns relating diet diversity and variation which may help identify future direction in examining effects of large scale landscape changes such as agricultural land use on aerial insectivore diet and foraging patterns.

3.4.2 Adult versus Nestling Diets

Insects from the aquatic orders Diptera and Odonata made up the majority of the diet for adult and nestling swallows at all sites. However, the diet of nestlings included larger proportions of "Terrestrial Diptera" and nestlings had larger isotopic niches than adults across all sites and years. A larger isotopic niche width in the nestlings may simply be due to consumption of a wider variety of prey compared to the adults or increased variation in the isotopic values of the prey sources during the period of nestling growth (Matthews and Mazumder 2004). Age class differences could also be related to 1) changes in the isotopic signature of the food web over time, 2) adults feeding their nestlings a different diet due to higher energetic demands during the nestling period, 3) food quality, or 4) temporal changes in the emergence patterns of the insect community. Due to logistical constraints, I was unable to sample the diet of adult and nestling tree swallows at the same time (approximately 12 days apart). However, I was careful to collect insects at times that would align with isotopic measurements of swallow red blood cells. There was little change in the stable isotope values of insects over the breeding season and red blood cells have an integrated isotopic signal of diet over 2–3 weeks which suggests that the differences in the diet proportions of adults and nestlings are real and not an artifact of temporal shifts in the carbon and/or nitrogen isotope composition of the baseline food web. The swallow

nest boxes are situated along roadside ditches which are dominated by terrestrial, non-native grasses and perennials that may accommodate high insect diversity. Foraging demands during the nestling period may force adults to forage closer to the nest box where they select less preferred but locally abundant prey. This may result in nestlings consuming a larger variety of insects while adults early in the season have greater flexibility to forage for preferred, aquatic prey.

Additionally, nutritional quality of the prey may motivate age-related divergence in the diet. In other systems, acorn woodpecker (*Melanerpes formicivorus*) adults feed their nestlings a much higher proportion of insects while they forage primarily on acorns, potentially as a result of local availability of insects and acorn stores and higher protein content of insects versus acorns (Koening et al. 2008). Further investigation of the nutritional content of swallow diet sources would provide insight on mechanisms or consequences for diet variation between age classes in areas affected by agricultural land use and may explain the slightly higher δ^{15}N values for nestlings. Finally, temporal shifts in the emergence patterns and abundance of the insect community may be driving the increase in the proportion of "Terrestrial Diptera" and larger isotopic niches from adults to nestlings. Adult and nestling tree swallows eat primarily insects from "Aquatic Orders" suggesting this is likely the preferred prey, which is consistent with other studies (Quinney and Ankney 1985, Blancher and McNicol 1988, McCarty and Winkler 1999a, Beck et al. 2013). Rather than reducing their brood size, typical during poor conditions, adults fed their nestlings more "Terrestrial Diptera", suggesting that they may be adjusting to temporal changes in insect community. I speculate that environmental conditions that alter availability of aquatic prey may have important impacts on diet and composition with consequences for tree swallow reproductive success or survival.

3.4.3 Assimilated Diet and Body Condition

There was a trade-off between the two prey sources, "Aquatic Orders" and "Terrestrial Diptera", within the diet of swallows of all age groups and years. The larger the proportion of insects consumed from "Aquatic Orders", the smaller proportion of "Terrestrial Diptera" and vice versa. These two main diet sources had similar δ^{15}N values, but varied in δ^{13}C, with "Aquatic Orders" having more negative values, providing an opportunity to test for variation in body condition between the prey sources. None of the body condition responses measured was consistently related to the isotopic diet of swallows. Although land type was in the best-approximating models explaining adult body mass and condition, the effect sizes were small. In a more direct analysis that was not focused on adult diet, adult body condition was unrelated to agricultural land use (Stanton 2015), which is consistent with another study of tree swallow populations in eastern Canada, where food abundance was observed at agriculturally intensive sites (Rioux Paquette et al. 2014). My results may indicate that swallows are able to adjust their diet to maintain condition and that both aquatic and terrestrial Diptera species are adequate prey options. Perhaps adults are foraging more frequently or further to meet the demands of nestling growth as foraging rates were positively related to nestling age (Stanton 2015). Nestlings typically showed a more diverse and generalist diet than adults, consisting of dipteran prey, suggesting that the amount of food they receive may be much more important to short term growth and condition than whether it is from an aquatic or terrestrial source. Previous work has shown that nestling tree swallows are often fed Diptera prey along with a variety of other aquatic and terrestrial prey and the proportions which they receive are related to the surrounding habitat and do not change seasonally (Beck et al. 2013). For example, Odonata and Ephemeroptera are

more common in the diet of nestlings raised near wetlands versus drier habitats (Johnson and Lombardo 2000, Mengelkoch et al. 2004).

Agricultural land use at the sites in this study may not have reduced the insect population sufficiently to cause a major diet shift to non-Dipteran prey which subsequently will not result in a diet-influenced reduction in body condition. In Chapter 2, I found that nestling body condition to be consistently lower at agricultural sites but no evidence was found to suggest that their mass, size and condition were closely related to diet. It appears that swallows at agricultural sites are able to forage on similar prey as those at the reference site. Semi-natural areas likely provide higher densities of aerial insects and swallows forage selectively in these areas. Song sparrow (*Melospiza melodia*) nestlings raised in an agricultural habitat had a large proportion of insects from semi-natural areas in their diet while these areas made up a very small proportion of the surrounding landscape available for foraging (Girard et al. 2012). Barn swallows foraged selectively at agricultural field boundaries, particularly during bad weather or when the adjacent field was winter wheat, and boundary areas containing hedgerows and trees offered higher food availability (Evans et al. 2003).

3.4.4 Conclusions

Using stable isotope techniques, I was not able to discern any clear effects of agricultural land use on tree swallow diet, dietary niche breadth, and diet-related body measurements and condition. Diet and niche widths showed variation among sites but the relationships changed both within and among sites from year to year. Subtle local habitat differences such as crop type, amounts and types of pesticides used and area of trees and wetlands are subject to change from year to year and could affect local insect abundance and emergence patterns. Tree swallows may

also be selectively foraging in semi-natural habitats where refuge habitat is provided for high insect abundance which may be sufficient to offset potential reductions in insects in the cropland. Thus, from this study and other previous work, tree swallows appear to be Diptera specialists but habitat generalists and are able to adjust their diet with habitat changes (Durst et al. 2008, Alberts et al. 2013, Beck et al. 2013). All study sites had an abundance of wetlands and some uncultivated terrestrial habitat, both of which will produce Diptera prey. Swallows appear to be flexible and able to compensate for potential reductions in the aquatic prey by feeding more on insects produced in terrestrial habitats. Given that both years of the study were affected by a record-breaking, multi-year flooding event, it would be interesting to test tree swallow's dietary responses in other extreme weather such as a drought, or during relatively typical arid Prairie conditions. In general, I was able to confirm that the diet of adult and nestling tree swallows was different across multiple sites varying in levels of agricultural land use. Consistent with other studies on aerial insectivores, it is likely that the major limiting factor for short-term reproductive success and condition of tree swallows is prey availability over diet composition, though long term effects of diet selection and quality of aquatic and terrestrial prey sources have yet to be determined.

CHAPTER 4: SYNTHESIS

Species of declining aerial insectivores occur across multiple ecosystems throughout North America and are exposed to different stressors. One factor linking this geographically and ecologically widespread guild is their high reliance on aerial insects. Many factors may affect abundances of aerial insects in North America and Europe, and agricultural land use is no exception. Research in Europe has found direct and indirect effects of agricultural land use on occurrence, reproductive success, body condition, and foraging patterns of many passerines, including aerial insectivores (Rodenhouse and Best 1994, Brickle et al. 2000, Donald et al. 2001, Ambrosini et al. 2002, Evans et al. 2007, Ghilain and Bélisle 2008, Girard et al. 2012, Rioux Paquette et al. 2014). In many areas, including the Canadian Prairies, agriculture has shifted from small family farms to larger corporate farming operations and land use has transitioned with this shift (Bélanger and Grenier 2002, Batáry et al. 2010). Intensive agriculture practices are likely to continue, expanding agricultural landscapes in the future, creating an immediate need to understand how these changes may directly or indirectly affect non-target organisms, such as avian aerial insectivores.

I examined the reproductive ecology and nestling body condition of the aerial insectivore species, the tree swallow, across five study sites varying in levels of agricultural land use. As well, I looked at potential dietary shifts of adult and nestling swallows to infer a possible mechanism linking agricultural land use to populations of aerial insectivores through prey reductions or changes in their diet. I anticipated that abundances of aerial insects would be lower at agricultural sites resulting in tree swallows occupying these sites at lower densities, breeding later, and having lower reproductive success. In turn, I expected that adult swallows would respond to reductions in aerial insect abundance at agricultural sites by incorporating less

preferred prey type in their diet and their nestling's diet, or by working harder to acquire preferred prey, resulting in lower body condition in adults and nestlings.

There was no effect from agricultural land use on aerial insect abundance or biomass as measured with passive insect samplers and subsequently no effects on the occupancy rates and reproductive ecology of swallows between agricultural and reference sites. Traditional passive aerial insect samplers which have been used for decades at St. Denis as well as other tree swallow colonies across Canada are valuable for within site comparisons but can be challenging for between site comparisons due to small-scale landscape differences (Hussell and Quinney 1987). Vertical structures such as hedgerows and trees act as wind breaks to protect insects from dispersal but many of these landscape features have been removed due to changes in land use to cropland, allowing higher insect dispersal and increasing the likelihood of capture in our passive nets. Alternatively, trees at reference sites have not been removed, corralling insects into sheltered areas that have higher abundances of aerial insects, including Chironomidae species of the order Diptera (Delettre and Morvan 2000), resulting in higher foraging rates in these areas (Girard et al. 2012). Thus, samples from the passive insect samplers may not be representative for what is available to the swallows.

Swallows are vulnerable to increased metabolic demands and reduced food availability due to cold temperatures or precipitation (McCarty and Winkler 1999b, Winkler et al. 2013). Insect flight activity is hindered during poor environment conditions (Taylor 1963, Dunn et al. 2011). Close proximity (~80 km) between study sites produces similar daily environmental conditions from weather, suggesting that insects are exposed to the same conditions between sites. Given the temperature dependence of insect flight, effects from agricultural land use may be masked by inclement weather across all sites. If agricultural land use did negatively affect

aerial insect biomass and abundance, we would expect to see an effect on tree swallow productivity. The lack of an effect on swallow reproductive measures suggests that agricultural land use did not negatively affect aerial insects to the extent that they may limit swallow reproduction. Alternatively, analogous effects from environmental conditions across all sites may have overwhelmed effects from agricultural land use.

Consistent with other studies, tree swallows foraged primarily on the orders Odonata and Diptera, the latter being from both aquatic and terrestrial origins (McCarty and Winkler 1999a, Johnson and Lombardo 2000, Mengelkoch et al. 2004). They did not consistently switch to primarily terrestrial based orders such as Hemiptera and Hymenoptera at agricultural sites suggesting that either availability of preferred prey, Odonata and Diptera, was sufficient across sites or tree swallows remain selective. The diet of adults and nestlings consisted mainly of "Aquatic Orders" but prey proportions and niche widths were significantly different. Seasonal shifts in foraging strategies or diet selection of the adults potentially could have caused a divergence in the diet proportions of adults and nestlings and these shifts could be a result of 1) seasonal changes in the availability of the two prey types; 2) adults attempting to meet increased foraging demands from nestlings; 3) differences in the nutritional requirements between the two age classes. Future work may consider sampling adults and nestlings concurrently. A similar diet between the age classes, sampled concurrently, would support the first hypothesis but require more investigation. Additionally, adult swallows increased foraging trips when food availability was high and with nestling age (Stanton, 2015). Therefore, if a disparity in the diet remained, then it may be due to higher foraging demands during the nestling period. Finally, differences in the diet of adults and nestlings which were sampled concurrently could reflect nutritional requirement during nestling growth. Alternatively, using multiple tissues or multiple sampling

times of individuals will also provide information on diet disparities due to effects from the environment or parental foraging strategies.

My most intriguing result was the lower body condition of nestlings raised on agricultural sites relative to reference sites for 1655 nestlings. Although insect availability is important for nestling quality in tree swallows (Ardia 2006), parental quality can also be a factor (Harriman 2014). Yet, I did not find that nestling body condition was related to parental age or experience. The amount of time adults spent foraging during nestling growth was greater at agricultural sites but neither adult body condition nor adult foraging rates were lower at agricultural sites (Stanton 2015), indicating that reduced nestling condition at agricultural sites may not be strongly influenced by parental quality. This is consistent with an experimental study that found lower foraging rates of adults with clipped wings (reducing their quality) had no effect on nestling mass (Winkler and Allen 1995). I found no indication that diet influenced their condition as nestlings across all sites consumed mostly Odonata and Diptera and their assimilated diet was not related to body condition. The nutritional content of aquatic and terrestrial Diptera may be similar, and foraging may be based on the availability of Diptera insects from these distinct life cycles. However, non-essential elements and toxicants could be incorporated in the prey items at agricultural sites (Haroune et al. 2015) and have a negative effect on nestling quality. A recent study found oil seed rape insect pests which were consumed by common swifts had higher levels of arsenic (Orłowski et al. 2015). Additionally, levels of polychlorinated biphenyls (PCBs) and dichlorodiphenyltrichloroethane (DDT) in adult and nestling swallows were related to the amount of aquatic or terrestrial prey in their diet; consumption of terrestrial prey resulted in higher concentrations of DDT in the tissues while PCBs were found when consuming an aquatic diet (Smits et al. 2005). Nestlings in my study may have ingested more pesticides at agricultural

sites as the timing of agrochemical applications is closer to the nestling period than the time when adults were sampled. Although Diptera are very sensitive to pesticides (Morrissey et al. 2015), those collected from swallow boluses in an agricultural landscape in Québec did contain multiple classes of insecticides (Haroune et al. 2015), including neonicotinoids which are more commonly found in agricultural wetlands at our study (Chapter 2). Testing of insect prey or swallow fecal samples for pesticides or non-essential elements would help determine if contaminants could be impairing nestling body condition at agricultural sites in Saskatchewan. Such finding would be important to agriculture because of increased agrochemical use in recent years for higher crop yields.

4.1 ALTERNATIVES TO AGRICULTURAL INTENSIFICATION

Concerns stemming from a projected population of 9 billion humans by 2050, have promoted further agricultural intensification to meet increased food demands over a proposed alternative to reduce intensive farming practices but increase agricultural area (extensification) to counter yield losses (Godfray et al. 2010, Tscharntke et al. 2012). Even if landowners were in favour of less intensive practices, in some cases, they have little choice than to use unstainable methods because of market saturation. Increased applications of pesticides, particularly systemic insecticides, are frequently used as an insurance policy; applied yearly regardless of level of threat from pests. In Canada, 95% of canola seeds are treated with neonicotinoids, leaving few options for landowners. As well, crop yields do not improve with blanket applications of pesticides, such as neonicotinoids, adding unnecessary costs to landowners and threaten non-target insects and higher trophic consumers in agricultural landscapes (Myers and Hill 2014).

Removal and degradation of natural habitats and wetland drainage continues despite warnings of the ecological and agricultural services they provide for pest management, pollination, nutrient cycling and retention, and flood and drought protection (Altieri 1999, Bartzen et al. 2010, Power 2010, Wezel et al. 2014). Intensive agricultural practices are shifting away from integrated pest management (IPM) practices which include both chemical and biological control agents for pest management (Stern et al. 1959). Good growing conditions and fair pay outs of popular crops planted in Saskatchewan (i.e., canola, wheat, barley) has encouraged reduced crop rotations and increased the use of pesticides and fertilizers to suppress pest outbreaks and maintain soil nutrients. These technological advances in agriculture have helped to propagate these conventional farming practices. However, many pesticides negatively affect non-target insects that are beneficial for biological control of agricultural pest insects (O'Rourke et al. 2011) resulting in reductions in crop yield (Douglas et al. 2014, Gasper et al. 2014). Alternative methods such as retaining uncultivated habitats, increased crop diversification, nutrient management and biological control are effective pest management practices while maintaining crop yields (Matson et al. 1997, Thies and Tscharntke 1999, Bianchi et al. 2006, Gardiner et al. 2009). Wetland loss due to drainage for agricultural expansion continues (Watmough and Schmoll 2007) despite warnings that drainage increases surface water area in wetlands relative to those landscapes with no drainage (McCauley et al. 2015). Reduction in wetland density in the Prairie Pothole Region may be irreversible and have long-term negative effects to landowners and the environment when combined with predicted wetland losses due to warmer and drier weather from climate change (Withey and van Kooten 2011) or leave landscapes vulnerable to largescale flooding associated with more extreme precipitation events. Incorporating landscape complexity by increasing the area of non-cropped habitat such as grassy

ditches and wetlands promote favourable farming conditions while providing habitat for many taxa, including avian species that are important for ecosystem services where they can help reduce pest outbreaks (Whelam et al. 2008).

4.2 IMPLICATIONS TO AERIAL INSECTIVORE CONSERVATION

Although I was unable to conclusively link aerial insect availability as the indirect mechanism explaining lower nesting body condition on agricultural sites, this work is an important contribution for aerial insectivore conservation. During my study, the Canadian Prairies experienced record-breaking spring run-off and rainfall events. Arthropod abundance is negatively affected by spring drought conditions (Frampton et al. 2000) and, in swallows, apparent annual survival of nestlings is positively related to conditions of soil moisture conditions and wetlands (Harriman 2014). Furthermore, recruitment rates of tree swallows are lower for lighter and smaller birds (Shutler et al. 2006, Harriman 2014) as well as many other avian species (Brinkhof et al. 1997, Both et al. 1999, Monrós et al. 2002, Medeiros and Freed 2009). The diet of swallows varied across study sites; however, variation was restricted to traditionally dominant prey types, Odonata and Diptera (aquatic and terrestrial) and their diet was unrelated to nestling body condition. Further studies are encouraged to examine other potential linkages between agricultural land use and aerial insectivore declines. A promising area may be contaminant ingestion (i.e., pesticides) as some toxic compounds including two neonicotinoids, clothianidin and thiamethoxam, have been detected in food boluses of tree swallows (Haroune et al. 2015). As well, long-term monitoring is needed to better understand additive effects of landscape changes and environmental extremes (i.e., drought) on aerial insectivore declines. Adequate insect availability due to semi-natural habitats may be perceived by some that agriculturally intensified landscapes are good nesting habitat. However, these areas

could be ecological traps for tree swallows or other aerial insectivore species if the birds which are attracted to these areas produce nestlings of lower condition, which may affect overall recruitment and potential population declines.

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Appendix 1. Percent area of crop, grass (native/ non-native and pasture), trees, water, and infrastructure (i.e., building, roads, gravel pits), and mean neonicotinoid concentration at 6 tree swallow study sites in south-central Saskatchewan. N is the number of quarter sections.

Land Type	Site	N	Crop	Grass	Trees	Water	Infrastructure	Neonicotinoid Concentration[1]
Agriculture	Burr	5	79.3	13.6	1.0	5.0	1.2	97.5
	Colonsay 2012	4	71.7	11.6	11.4	4.1	1.1	16.4
	Colonsay2013	4	79.7	5.2	2.7	10.0	2.4	21.3
	Humboldt	5	57.2	11.4	2.9	24.5	4.0	360.8
Reference	St. Denis	5	4.3	72.3	5.1	13.2	0.1	2.14
	Allan	3	0	67.2	9.2	22.5	1.1	0.10

[1] Concentrations in ng/L.

Appendix 2. Model selection results for clutch initiation date (CID), clutch size, brood size, number of nestlings fledged, and nestling body condition index. Explanatory variables include year, land type (land; agriculture versus reference), nest box type, female experience (f.recap), and clutch initiation date (except for CID model). Models testing variation in clutch initiation date, clutch size, brood size, and number of nestlings fledged were completed using general linear models with a Poisson distribution. Linear mixed effects models with nest box as random factor were completed to test nestling body condition index. Only models with a weight greater than 0 and the intercept model (null) are included.

Response	Model Structure[1]	K[2]	AIC_c[3]	ΔAIC_c[4]	Deviance[5]	w_i[6]
	null	1	2165.04	0.00	2163.02	0.28
	f.recap	2	2166.24	1.20	2162.20	0.15

Clutch Initiation Date	land	2	2166.95	1.92	2162.92	0.11
	box.type	2	2167.06	2.02	2163.02	0.10
	box.type + f.recap	3	2168.27	3.24	2162.20	0.06
	land + f.recap	3	2168.28	3.24	2162.20	0.06
	land + box.type	3	2168.99	3.95	2162.90	0.04
	year	3	2169.09	4.05	2163.02	0.04
	box.type + f.recap + box.type × f.recap	4	2170.14	5.1	2162.00	0.02
	year + f.recap	4	2170.31	5.27	2162.18	0.02
	land + f.recap + land × f.recap	4	2170.32	5.28	2162.18	0.02
	land + box.type + land × box.type	4	2171.03	6.00	2162.90	0.01
	year + land	4	2171.04	6.00	2162.90	0.01
	year + box.type	4	2171.14	6.10	2163.00	0.01
	land + box.type + f.recap + box.type × f.recap	5	2172.20	7.16	2162.00	0.01
	year + box.type + f.recap	5	2172.37	7.33	2162.18	0.01
	year + land + f.recap	5	2172.37	7.33	2162.18	0.01
	land + box.type + f.recap + land × box.type	5	2172.38	7.34	2162.18	0.01
	land + box.type + f.recap + land × f.recap	5	2172.38	7.34	2162.18	0.01
Clutch Size	CID	2	1168.57	0.00	1164.52	0.28
	CID + f.recap	3	1170.29	1.73	1164.22	0.12

CID + box.type	3	1170.59	2.02	1164.50	0.10
land + CID	3	1170.61	2.04	1164.52	0.10
CID + box.type + f.recap	4	1172.33	3.76	1164.20	0.04
land + CID + f.recap	4	1172.33	3.76	1164.20	0.04
land + CID + box.type	4	1172.64	4.07	1164.50	0.04
year + CID	4	1172.64	4.07	1164.50	0.04
land + CID + land × CID	4	1172.66	4.09	1164.52	0.04
null	1	1173.43	4.86	1171.42	0.02
land + CID + box.type + f.recap	5	1174.38	5.81	1164.18	0.02
land + CID + f.recap + land × CID	5	1174.39	5.82	1164.18	0.02
year + CID + f.recap	5	1174.41	5.84	1164.20	0.01
year + CID + box.type	5	1174.68	6.11	1164.48	0.01
land + CID + box.type + land × CID	5	1174.70	6.13	1164.50	0.01
year + land + CID	5	1174.71	6.14	1164.50	0.01
f.recap	2	1174.78	6.21	1170.74	0.01
land	2	1175.44	6.87	1171.40	0.01
box.type	2	1175.44	6.87	1171.40	0.01
land + CID + box.type + f.recap + land × CID	6	1176.45	7.88	1164.16	0.01
year + CID + box.type + f.recap	6	1176.46	7.89	1164.18	0.01
year + land + CID + box.type	6	1176.47	7.90	1164.18	0.01

Brood Size	CID	2	1189.07	0.00	1185.02	0.24
	CID + f.recap	3	1190.26	1.20	1184.18	0.13
	CID + box.type	3	1190.98	1.91	1184.90	0.09
	CID + land	3	1191.08	2.02	1185.00	0.09
	CID + land + f.recap	4	1192.12	3.06	1184.00	0.05
	CID + box.type + f.recap	4	1192.19	3.13	1184.06	0.05
	CID + year	4	1192.24	3.18	1184.12	0.05
	CID + land + box.type	4	1192.24	3.18	1184.12	0.05
	CID + land + CID × land	4	1193.14	4.07	1185.00	0.03
	CID + year + f.recap	5	1193.62	4.55	1183.42	0.02
	CID + land + box.type + f.recap	5	1194.08	5.01	1183.88	0.02
	CID + land + f.recap + CID × land	5	1194.19	5.12	1183.98	0.02
	CID + year + box.type	5	1194.29	5.22	1184.08	0.02
	CID + land + year	5	1194.30	5.23	1184.10	0.02
	null	1	1194.79	5.72	1192.78	0.01
	CID + land + box.type + CID × land	5	1195.08	6.01	1184.88	0.01
	f.recap	2	1195.38	6.31	1191.34	0.01
	CID + land + year + f.recap	6	1195.56	6.49	1183.28	0.01
	CID + year + box.type + f.recap	6	1195.68	6.61	1183.40	0.01
	CID + land + box.type + f.recap + CID × land	6	1196.16	7.09	1183.88	0.01

	CID + year + CID × year	6	1196.16	7.09	1183.88	0.01
	CID + land + year + box.type	6	1196.36	7.29	1184.07	0.01
	CID + land + year + CID × land	6	1196.38	7.31	1184.10	0.01
	box.type	2	1196.69	7.63	1192.66	0.01
	land	2	1196.81	7.75	1192.66	0.01
Number of Fledged Nestlings	CID + f.recap	3	1279.44	0.00	1273.36	0.24
	CID + land + f.recap	4	1280.94	1.51	1272.82	0.11
	CID	2	1281.32	1.89	1277.28	0.09
	CID + box.type + f.recap	4	1281.40	1.96	1273.26	0.09
	CID + year + f.recap	5	1282.67	3.23	12.72.46	0.05
	CID + land + box.type + f.recap	5	1282.94	3.50	1272.74	0.04
	f.recap	2	1282.98	3.54	1278.94	0.04
	CID + land + f.recap + CID × land	5	1283.00	3.57	1272.80	0.04
	CID + box.type	3	1283.27	3.83	1277.18	0.04
	CID + land	3	1283.35	3.91	1277.26	0.03
	CID + year	4	1284.13	4.69	1276.00	0.02
	CID + land + year + f.recap	6	1284.31	4.87	1272.02	0.02
	CID + land + year + f.recap + year × land	8	1284.68	5.25	1268.20	0.02
	CID + year + box.type + f.recap	6	1284.74	5.31	1272.46	0.02
	CID + land + box.type + f.recap + CID × land	6	1285.01	5.58	1272.72	0.01

	CID + land + box.type	4	1285.31	5.87	1277.18	0.01
	CID + land + CID × land	4	1285.38	5.95	1277.24	0.01
	null	1	1285.96	6.52	1283.94	0.01
	CID + year + box.type	5	1286.19	6.75	1275.98	0.01
	CID + land + year	5	1286.19	6.75	1275.98	0.01
	CID + year + f.recap + year × CID	7	1286.31	6.88	1271.94	0.01
	CID + land + year + f.recap + CID × land	7	1286.38	6.95	1272.00	0.01
	CID + land + year + box.type + f.recap + year × land	9	1286.77	7.33	1268.16	0.01
	CID + land + year + year × land	7	1286.80	7.36	1272.42	0.01
	CID + land + year + f.recap + year × land + CID × land	9	1286.80	7.37	1268.20	0.01
Nestling Body Condition Index	CID + hatched + box.type + land+ CID × hatched	8	5795.14	0.00	5779.06	0.15
	CID + hatched + box.type + land + year + CID × hatched	10	5795.90	0.76	5775.76	0.10
	CID + hatched + box.type + land	7	5796.54	1.39	5782.48	0.07
	CID + hatched + box.type + land + year	9	5796.73	1.59	5778.62	0.07
	CID + hatched + box.type + land + f.recap + CID × hatched	9	5797.04	1.90	5778.92	0.06
	CID + hatched + box.type + land + year + year × CID	11	5797.78	2.64	5775.62	0.04
	CID + hatched + box.type + CID × hatched	7	5797.79	2.64	5783.72	0.02
	CID + hatched + box.type + land + year + f.recap + CID × hatched	11	5797.90	2.76	5775.74	0.04
	CID + hatched + box.type + land + year + f.recap + year × land × CID	17	5798.22	3.08	5763.84	0.03
	CID + hatched + box.type + land + f.recap	8	5798.39	3.25	5782.30	0.03

CID + hatched + box.type + land + CID × land	8	5798.56	3.41	5782.46	0.03
CID + hatched + box.type + land + year + year*land	11	5798.64	3.49	5776.48	0.03
CID + hatched + box.type + land + year + year × CID + land × CID	12	5798.64	3.50	5774.46	0.03
CID + hatched + box.type + land + year + CID × land	10	5798.73	3.58	5778.60	0.02
CID + hatched + box.type + land + year + f.recap	10	5798.73	3.58	5778.60	0.02
CID + hatched + box.type + year + CID × hatched	9	5799.10	3.96	5781.00	0.02
CID + hatched + box.type	6	5799.48	4.34	5787.42	0.02
CID + hatched + box.type + land + year + year × land + year × CID	13	5799.60	4.45	5773.38	0.02
CID + hatched + box.type + f.recap + CID × hatched	8	5799.62	4.47	5783.52	0.02
CID + hatched + box.type + land + year + f.recap + year × CID	12	5799.74	4.60	5775.56	0.01
CID + hatched + box.type + year	8	5800.27	5.13	5784.18	0.01
CID + hatched + box.type + f.recap + CID × land	9	5800.41	5.26	5782.30	0.01
CID + hatched + box.type + land + year + f.recap + year × CID + land × CID	13	5800.54	5.40	5774.32	0.01
CID + hatched + box.type + land + year + f.recap+ year × land	12	5800.55	5.41	5776.36	0.01
CID + hatched + box.type + land + year + year × land + land × CID	12	5800.65	5.50	5776.46	0.01
CID + hatched + box.type + year + f.recap + CID × hatched	10	5800.69	5.55	5780.56	0.01
CID + hatched + box.type + land + year + f.recap + CID × land	11	5800.72	5.58	5778.56	0.01
CID + box.type + land	6	5801.02	5.88	5788.96	0.01
CID +box.type + land + year	8	5801.09	5.94	5785.00	0.01

CID + hatched + box.type + f.recap	7	5801.33	6.19	5787.26	0.01
CID + hatched + box.type + land + year + f.recap + year × land + year × CID	14	5801.47	6.32	5773.22	0.01
CID + box. type + land + year × CID	10	5801.73	6.58	5781.60	0.01
CID + hatched + box.type + year + year × CID	10	5801.82	6.67	5781.68	0.01
CID + hatched + box.type + year + f.recap	9	5801.85	6.71	5783.74	0.01
null	3	5820.19	25.04	5814.18	0.00

[1] Explanatory variables included year, land type (agriculture, reference), clutch initiation date (CID), female experience (f.recap), and nest box type.

[2] Number of estimable parameters.

[3] Akaike's Information Criterion, corrected for small sample sizes.

[4] Difference in AIC_c between each model and the model with the lowest AIC_c value.

[5] -2 × Log Likelihood.

[6] Model weight.

Appendix 3. Model selection results for insect abundance and insect biomass index (IBI) during CID, egg laying and nestling period. Only models with a weight greater than 0 and the intercept model (null) are included.

Response	**Model Structure[1]**	**K[2]**	**AIC_c[3]**	**ΔAIC_c[4]**	**Deviance[5]**	**w_i[6]**
Insect Abund. during CID	year + land + date + year × date	9	374.99	0.00	356.14	0.41
	year + date + year × date	8	376.17	1.19	359.50	0.23
	year + land + date + year × date + land × date	10	376.5	1.51	355.46	0.19
	year + land + date + year × land + year × date	11	377.53	2.55	354.28	0.12
	year + land + date + year × land+ year × date + land × date	12	379.42	4.44	353.94	0.04

	null	3	533.96	158.97	527.84	0.00
Insect Abund. during Egg Laying	year + date	6	388.53	0.00	376.06	0.30
	year + land + date	7	390.39	1.86	375.78	0.12
	year + land + date + land × date	8	390.47	1.95	373.69	0.12
	year + land + date + year × land	9	390.64	2.11	371.64	0.11
	year	5	390.71	2.18	380.38	0.10
	year + date + year × date	8	391.74	3.21	374.94	0.06
	year + land + date + year × land + land × date	10	392.26	3.73	371.04	0.05
	year + land	6	392.62	4.10	380.16	0.04
	year + land + year × land	8	393.19	4.66	376.40	0.03
	year + land + date + year × date	9	393.64	5.11	374.64	0.02
	year + land + date + year × date + land × date	10	393.97	5.44	372.74	0.02
	year + land + date + year × land + year × date	11	393.97	5.44	370.50	0.02
	year + land + date + year × land+ year × date + land × date	12	395.74	7.21	369.98	0.01
	null	3	400.08	11.55	393.96	0.00
Insect Abund. during Nestling Period	year + land + date + year × date	9	686.78	0.00	668.20	0.50
	year + land + date + year × date + land × date	10	688.68	1.91	667.96	0.19
	year + land + date + year × land + year × date	11	689.04	2.26	666.18	0.16
	year + land + date + year × land+ year × date + land × date	12	690.71	3.93	665.70	0.07

	year + land + date + year × land+ year × date + land × date + year × land × date	14	690.86	4.08	664.46	0.07
	null	2	777.8	91.12	771.82	0.00
IBI during CID	year + date + year × date	8	555.54	0.00	538.86	0.54
	year + land + date + year × date	9	557.14	1.60	538.30	0.24
	year + land + date + year × date + land × date	10	558.61	3.07	537.58	0.12
	year + land + date + year × land + land × date	11	559.69	4.15	536.44	0.07
	year + land + date + year × land+ year × date + land × date	12	561.35	5.81	535.86	0.03
	null	3	670.75	115.21	664.64	0.00
IBI during Egg Laying	year + date	6	494.70	0.00	482.24	0.47
	year + land + date	7	496.84	2.14	482.22	0.16
	year + land + date + land × date	8	497.70	3.00	480.9	0.10
	year	5	498.52	3.82	488.20	0.07
	year + date + year × date	8	498.84	4.14	482.04	0.06
	year + land + date + year × land	9	499.33	4.63	480.34	0.05
	year + land	6	500.65	5.95	488.20	0.02
	year + land + date + year × date	9	501.02	6.32	482.02	0.02
	year + land + date + year × land + land × date	10	501.19	6.49	479.98	0.02
	year + land + date + year × date + land × date	10	501.97	7.27	480.74	0.01
	year + land + year × land	8	503.27	8.57	486.48	0.01

	year + land + date + year × land + year × date	11	503.61	8.91	480.14	0.01
	null	3	524.62	29.92	518.5	0.00
IBI during Nestling Period	year + land + date + year × date	9	881.8	0.00	863.22	0.36
	year + date + year × date	8	882.72	0.92	866.26	0.23
	year + land + date + year × land + year × date	11	883.53	1.73	860.66	0.15
	year + land + date + year × date + land × date	10	883.86	2.06	863.14	0.13
	year + land + date + year × land+ year × date + land × date	12	885.46	3.66	860.44	0.06
	year + land + date + year × land+ year × date + land × date + year × land × date	14	886.14	4.34	856.76	0.04
	year + land + date	7	889.03	7.23	874.66	0.01
	year + date	6	889.29	7.49	877.02	0.01
	null	3	949.56	67.76	943.48	0.00

[1] Explanatory variables included year, land type (agriculture, reference), date (mean-centered).

[2] Number of estimable parameters.

[3] Akaike's Information Criterion, corrected for small sample sizes.

[4] Difference in AIC_c between each model and the model with the lowest AIC_c value.

[5] -2 × Log Likelihood.

[6] Model weight.

Appendix 4. Model selection results for abundances of aquatic and terrestrial Diptera. Only models with a weight greater than 0 and the intercept model (null) are included.

Response	Model Structure[1]	K[2]	AIC_c[3]	ΔAIC_c[4]	Deviance[5]	w_i[6]
Abund. Aquatic Diptera	land + habitat + sample period	8	93.38	0.00	70.18	0.75
	habitat + sample period	7	97.04	3.67	77.72	0.12
	land + habitat	6	98.06	4.68	82.24	0.07
	land + habitat + sample period + land × habitat	10	100.49	7.12	68.28	0.02
	habitat	5	100.59	7.21	87.98	0.02
	land + sample period	6	101.51	8.14	85.70	0.01
	null	3	107.40	14.02	100.44	0.00
Abund. Terrestrial Diptera	land + habitat	6	136.81	0.00	122.70	0.58
	habitat	5	138.11	1.30	126.64	0.07
	land + habitat + sample period	8	140.94	4.13	121.14	0.07
	habitat + sample period	7	142.73	5.92	125.86	0.03
	habitat + sample period + habitat × sample period	10	145.67	8.86	119.56	0.01
	null	3	164.60	27.79	158.01	0.00

[1] Explanatory variables included land type (agriculture, reference), habitat (upland, wetland and ditch), and sample period (incubation, hatch, nestling period).

[2] Number of estimable parameters.

[3] Akaike's Information Criterion, corrected for small sample sizes.

[4] Difference in AIC_c between each model and the model with the lowest AIC_c value.

[5] -2 × Log Likelihood.

[6] Model weight.

Appendix 5. Total number of transects (N), mean ± SD of $\delta^{13}C$ and $\delta^{15}N$ (‰) and C:N ratios of insects orders and tree swallow red blood cells collected at 3 study sites in 2012. Agricultural sites include Burr (BUR), Colonsay (COL) while St. Denis (SD) is a reference site.

Order	Site	N	$\delta^{13}C$	$\delta^{15}N$	C:N
Aquatic Diptera	BUR	5	-26.61 ± 0.49	7.87 ± 1.18	4.56 ± 0.34
	COL	5	-27.98 ± 1.19	7.70 ± 0.65	4.75 ± 0.64
	SD	3	-28.74 ± 1.93	8.20 ± 1.62	4.57 ± 0.21
Terrestrial Diptera	BUR	4	-25.73 ± 0.85	10.12 ± 1.02	4.99 ± 0.39
	COL	4	-25.52 ± 0.56	9.07 ± 0.84	4.75 ± 0.21
	SD	3	-27.22 ± 1.04	7.67 ± 0.43	4.42 ± 0.12
Coleoptera	BUR	5	-26.57 ± 0.18	5.69 ± 1.64	4.99 ± 0.23
	COL	5	-26.69 ± 0.76	3.37 ± 0.60	4.69 ± 0.34
	SD	4	-26.71 ± 0.62	4.48 ± 0.21	4.85 ± 0.20
Hemiptera	BUR	5	-26.76 ± 0.91	6.09 ± 1.30	4.86 ± 0.24
	COL	5	-26.30 ± 0.82	1.87 ± 1.71	4.87 ± 0.19
	SD	3	-27.26 ± 0.28	5.21 ± 1.11	4.58 ± 0.07
Hymenoptera	BUR	2	-26.56 ± 0.24	7.21 ± 1.85	4.30 ± 0.29
	COL	2	-26.82 ± 0.75	4.71 ± 2.11	4.60 ± 0.35
	SD	2	-26.79 ± 0.46	7.16 ± 2.18	4.50 ± 0.07
Lepidoptera	BUR	3	-27.41 ± 0.59	6.36 ± 0.22	5.37 ± 1.30
	COL	4	-26.74 ± 0.01	6.32 ± 2.52	4.58 ± 0.42
	SD	3	-27.59 ± 0.01	3.80 ± 0.32	4.29 ± 0.62
Odonata	BUR	2	-28.17 ± 0.79	8.61 ± 0.44	4.23 ± 0.34
	COL	3	-28.48 ± 0.39	9.14 ± 0.69	4.26 ± 0.14
	SD	1	-29.65 ± 0.37	8.84 ± 0.30	4.30 ± 0.10
Orthoptera	BUR	5	-28.27 ± 0.57	2.59 ± 0.74	4.15 ± 0.32
	COL	5	-27.09 ± 1.16	1.56 ± 1.17	4.70 ± 1.12
	SD	4	-28.81	3.21	4.22
Tree Swallow Adults	BUR	29	-26.92 ± 0.46	11.09 ± 0.29	3.24 ± 0.01
	COL	35	-28.15 ± 0.44	10.41 ± 0.29	3.24 ± 0.01
	SD	51	-28.73 ± 0.40	10.89 ± 0.39	3.25 ± 0.02
Tree Swallow Nestlings	BUR	15	-25.77 ± 0.44	10.64 ± 0.28	3.24 ± 0.01
	COL	21	-26.75 ± 0.33	10.50 ± 0.35	3.25 ± 0.01
	SD	27	-27.48 ± 0.49	10.46 ± 0.35	3.25 ± 0.01

Appendix 6. Number of transects (N), mean ± SD of $\delta^{13}C$ and $\delta^{15}N$ (‰) and C:N ratios of insects orders and tree swallow red blood cells collected at 4 study sites in 2013. Agricultural sites include Burr (BUR), Colonsay (COL) and Humboldt (HUM) while St. Denis (SD) is a reference site.

Order	Site	N	$\delta^{13}C$	$\delta^{15}N$	C:N
Aquatic Diptera	BUR	27	-28.58 ± 1.14	8.19 ± 0.82	4.46 ± 0.24
	COL	24	-29.02 ± 1.34	8.81 ± 0.55	4.37 ± 0.23
	HUM	25	-29.28 ± 1.15	10.18 ± 1.25	4.34 ± 0.26
	SD	26	-29.6 1± 1.93	9.27 ± 0.96	4.40 ± 0.26
Terrestrial Diptera	BUR	25	-26.93 ± 1.34	8.96 ± 1.66	4.53 ± 0.27
	COL	25	-26.59 ± 1.47	8.73 ± 1.41	4.35 ± 0.30
	HUM	26	-26.64 ± 0.91	11.21 ± 2.65	4.49 ± 0.48
	SD	28	-26.80 ± 0.95	8.85 ± 1.28	4.48 ± 0.33
Coleoptera	BUR	22	-26.94 ± 0.80	8.54 ± 1.91	4.90 ± 0.61
	COL	22	-27.24 ± 0.85	7.86 ± 1.97	4.78 ± 0.45
	HUM	22	-27.52 ± 1.32	9.08 ± 2.31	4.70 ± 0.28
	SD	27	-27.01 ± 0.60	6.88 ± 1.76	4.98 ± 0.70
Hemiptera	BUR	23	-26.52 ± 0.90	7.06 ± 1.96	4.70 ± 0.38
	COL	20	-26.54 ± 0.81	8.00 ± 3.95	4.50 ± 0.37
	HUM	21	-26.91 ± 0.91	7.94 ± 2.81	4.77 ± 0.47
	SD	25	-26.76 ± 0.80	6.11 ± 2.50	4.43 ± 0.24
Hymenoptera	BUR	22	-28.46 ± 1.44	9.63 ± 2.10	4.57 ± 0.66
	COL	20	-27.94 ± 1.43	8.78 ± 3.59	4.23 ± 0.48
	HUM	21	-28.52 ± 1.23	11.73 ± 2.74	4.57 ± 0.75
	SD	25	-27.45 ± 0.92	7.61 ± 1.79	4.41 ± 0.76
Lepidoptera	BUR	8	-28.38 ± 0.56	5.33 ± 3.08	5.05 ± 1.02
	COL	8	-28.68 ± 0.50	6.08 ± 2.53	4.41 ± 0.32
	HUM	8	-29.03 ± 0.94	10.19 ± 2.47	4.87 ± 0.91
	SD	15	-29.05 ± 1.38	7.29 ± 2.40	4.56 ± 0.46
Odonata	BUR	12	-28.59 ± 0.91	8.93 ± 0.68	3.94 ± 0.17
	COL	18	-28.26 ± 1.02	10.56 ± 1.04	4.09 ± 0.17
	HUM	20	-28.89 ± 1.09	10.68 ± 1.46	4.17 ± 0.17
	SD	25	-29.69 ± 1.10	9.50 ± 1.06	4.09 ± 0.20
Orthoptera	BUR	10	-27.53 ± 0.89	5.12 ± 2.24	3.88 ± 0.28
	COL	10	-27.31 ± 1.09	5.89 ± 3.76	4.24 ± 0.67
	HUM	14	-27.32 ± 1.06	6.23 ± 2.72	3.90 ± 0.32
	SD	18	-27.64 ± 0.44	4.97 ± 1.88	4.16 ± 0.40
Tree Swallow Adults	BUR	48	-26.48 ± 0.34	11.02 ± 0.30	3.25 ± 0.02
	COL	39	-27.71 ± 0.58	11.51 ± 0.30	3.26 ± 0.10
	HUM	21	-27.51 ± 0.57	13.10 ± 0.51	3.24 ± 0.01
	SD	54	-27.94 ± 0.54	11.56 ± 0.29	3.24 ± 0.02
Tree Swallow Nestlings	BUR	23	-25.25 ± 0.35	10.99 ± 0.43	3.26 ± 0.02
	COL	21	-26.48 ± 0.75	11.44 ± 0.29	3.26 ± 0.02
	HUM	11	-26.96 ± 0.96	13.05 ± 0.54	3.27 ± 0.02
	SD	30	-27.57 ± 0.95	11.32 ± 0.55	3.26 ± 0.02

Appendix 7. Estimates (± S.E.) of *post-hoc* Tukey contrasts comparing the proportion of prey sources in the diet of swallows among study sites. Positive estimates indicate that swallows at site 1 had a higher proportion of the source in their diet than those at site 2. All comparisons were significant ($p < 0.001$) with the exception for those bolded.

Year	Age Class	Contrasted Sites		Aquatic Orders	Terrestrial Diptera	Terrestrial Orders
		Site 1	Site 2			
2012	Adults	Burr	Colonsay	- 0.14 ± 0.002	0.13 ± 0.003	0.06 ± 0.002
		Burr	St. Denis	0.11 ± 0.002	- 0.12 ± 0.003	- 0.01 ± 0.002
		Colonsay	St. Denis	0.26 ± 0.002	- 0.25 ± 0.003	- 0.07 ± 0.002
	Nestlings	Burr	Colonsay	- 0.19 ± 0.002	0.15 ± 0.003	0.10 ± 0.002
		Burr	St. Denis	0.15 ± 0.002	- 0.22 ± 0.003	0.08 ± 0.002
		Colonsay	St. Denis	0.35 ± 0.002	- 0.37 ± 0.003	- 0.02 ± 0.002
2013	Adults	Burr	Colonsay	- 0.25 ± 0.002	0.23 ± 0.002	0.09 ± 0.002
		Burr	Humboldt	- 0.23 ± 0.002	0.24 ± 0.002	0.04 ± 0.002
		Burr	St. Denis	- 0.12 ± 0.002	0.13 ± 0.002	0.02 ± 0.002
		Colonsay	Humboldt	0.03 ± 0.002	**0.01 ± 0.002**	- 0.05 ± 0.002
		Colonsay	St. Denis	0.12 ± 0.002	- 0.10 ± 0.002	- 0.07 ± 0.002
		Humboldt	St. Denis	0.10 ± 0.002	-0.11 ± 0.002	- 0.02 ± 0.002
	Nestlings	Burr	Colonsay	- 0.16 ± 0.002	0.12 ± 0.002	0.09 ± 0.002
		Burr	Humboldt	- 0.27 ± 0.002	0.23 ± 0.002	0.10 ± 0.002
		Burr	St. Denis	- 0.26 ± 0.002	0.23 ± 0.002	0.07 ± 0.002
		Colonsay	Humboldt	- 0.11 ± 0.002	0.12 ± 0.002	0.01 ± 0.002
		Colonsay	St. Denis	- 0.09 ± 0.002	0.12 ± 0.002	- 0.02 ± 0.002
		Humboldt	St. Denis	0.02 ± 0.002	**- 0.002 ± 0.002**	- 0.03 ± 0.002

Appendix 8. Summary statistics of estimated diet proportions of "Aquatic Orders", "Terrestrial Diptera" and "Terrestrial Orders" for adults and nestlings in 2012 and 2013 at 3–4 sites varying in levels of agricultural land use. The mean, S.D., and credible intervals (5%, 25%, 50%, 75%, and 95%) of the diet proportions are provided. Proportions were calculated using Bayesian mixing models in MixSIAR with separate insect samples collected at each site as sources.

			Adults							Nestlings						
Year	Site	Source	Mean	S.D.	5%	25%	50%	75%	95%	Mean	S.D.	5%	25%	50%	75%	95%
2012	Burr	Aquatic Orders	0.89	0.05	0.80	0.86	0.89	0.93	0.96	0.69	0.09	0.54	0.63	0.69	0.75	0.83
		Terrestrial Diptera	0.07	0.04	0.01	0.03	0.06	0.09	0.15	0.19	0.07	0.08	0.14	0.19	0.24	0.31
		Terrestrial Orders	0.04	0.03	0.01	0.02	0.04	0.06	0.10	0.12	0.06	0.03	0.07	0.11	0.16	0.23
	Colonsay	Aquatic Orders	0.96	0.03	0.91	0.94	0.97	0.98	0.99	0.85	0.06	0.75	0.81	0.85	0.89	0.94
		Terrestrial Diptera	0.02	0.01	<0.01	<0.01	0.01	0.02	0.04	0.09	0.05	0.02	0.05	0.08	0.12	0.18
		Terrestrial Orders	0.02	0.02	<0.01	<0.01	0.02	0.04	0.07	0.06	0.04	0.01	0.03	0.06	0.09	0.14
	St. Denis	Aquatic Orders	0.81	0.08	0.68	0.76	0.81	0.86	0.94	0.54	0.12	0.33	0.46	0.55	0.62	0.73
		Terrestrial Diptera	0.14	0.09	0.01	0.07	0.14	0.20	0.30	0.39	0.14	0.16	0.29	0.38	0.48	0.63
		Terrestrial Orders	0.05	0.04	<0.01	0.02	0.04	0.07	0.13	0.07	0.05	0.01	0.04	0.07	0.10	0.17
2013	Burr	Aquatic Orders	0.62	0.06	0.52	0.58	0.62	0.66	0.72	0.48	0.08	0.35	0.42	0.47	0.53	0.61
		Terrestrial Diptera	0.29	0.06	0.19	0.25	0.29	0.34	0.39	0.40	0.07	0.28	0.35	0.40	0.45	0.51
		Terrestrial Orders	0.09	0.03	0.04	0.07	0.09	0.11	0.15	0.13	0.06	0.04	0.08	0.12	0.16	0.22
	Colonsay	Aquatic Orders	0.84	0.06	0.74	0.80	0.84	0.88	0.93	0.63	0.08	0.51	0.58	0.63	0.68	0.76
		Terrestrial Diptera	0.12	0.05	0.04	0.08	0.11	0.15	0.21	0.29	0.08	0.16	0.24	0.29	0.35	0.43
		Terrestrial Orders	0.05	0.03	0.01	0.03	0.04	0.07	0.10	0.08	0.05	0.02	0.04	0.07	0.10	0.16
	Humboldt	Aquatic Orders	0.82	0.06	0.72	0.78	0.82	0.86	0.92	0.73	0.09	0.58	0.67	0.73	0.80	0.88
		Terrestrial Diptera	0.11	0.05	0.04	0.08	0.11	0.14	0.20	0.20	0.09	0.06	0.13	0.19	0.26	0.35
		Terrestrial Orders	0.07	0.05	0.01	0.03	0.06	0.10	0.16	0.07	0.06	0.01	0.03	0.06	0.10	0.18
	St. Denis	Aquatic Orders	0.74	0.04	0.67	0.71	0.74	0.77	0.81	0.72	0.06	0.62	0.68	0.72	0.76	0.82
		Terrestrial Diptera	0.18	0.05	0.11	0.15	0.18	0.22	0.26	0.20	0.07	0.08	0.15	0.19	0.24	0.32
		Terrestrial Orders	0.08	0.03	0.03	0.06	0.08	0.10	0.14	0.08	0.05	0.02	0.05	0.08	0.11	0.17

Appendix 9. Estimates, standard error (S.E.), Z scores, and p-values of post-*hoc* Tukey contrasts comparing the isotopic niche widths of adults and nestlings between study sites. Positive estimates indicate that site 1 has a larger niche width than site 2. All tests had a p-value < 0.001.

Year	Age Class	Contrasted Sites		Estimate	S.E.	Z Score
		Site 1	Site 2			
2012	Adults	Burr	Colonsay	0.08	0.003	29.94
		Burr	St. Denis	0.07	0.003	25.42
		Colonsay	St. Denis	- 0.01	0.003	- 4.51
	Nestlings	Burr	Colonsay	0.21	0.003	74.95
		Burr	St. Denis	0.04	0.003	15.85
		Colonsay	St. Denis	- 0.16	0.003	- 59.10
2013	Adults	Burr	Colonsay	- 0.49	0.003	- 175.30
		Burr	Humboldt	- 0.96	0.003	- 339.70
		Burr	St. Denis	- 0.22	0.003	- 78.45
		Colonsay	Humboldt	- 0.46	0.003	- 164.42
		Colonsay	St. Denis	0.27	0.003	96.84
		Humboldt	St. Denis	0.74	0.003	261.26
	Nestlings	Burr	Colonsay	- 0.41	0.003	- 146.73
		Burr	Humboldt	- 0.99	0.003	- 348.00
		Burr	St. Denis	- 0.95	0.003	- 336.74
		Colonsay	Humboldt	- 0.57	0.003	- 201.28
		Colonsay	St. Denis	- 0.54	0.003	- 190.01
		Humboldt	St. Denis	0.03	0.003	11.27

Appendix 10. Model selection results testing relationships between the isotopic values of red blood cells to mass, structural size (PC 1), and body condition index (BCI) of adults and nestling swallows using mixed effects models. Adults and nestlings were tested separately. Fixed effects included land type, sex (adults only), $\delta^{13}C$, $\delta^{15}N$ and their interactions. Site (nested in year), box type and date were included as random effects. Adults were analyzed as individuals (n=273) and nestlings as the mean of the three chicks sampled for blood in each nest box (n=145 nest boxes). Only models with $\Delta AIC_c < 0$ and the intercept-only model (null) are presented.

Age	Response	Model Structure	K[1]	AIC_c[2]	ΔAIC_c[3]	Deviance[4]	w_i[5]
Adults	Mass	land + sex	8	849.25	0.00	832.7	0.13
		land + sex + land × sex	9	849.92	0.68	831.24	0.09
		land + sex + $\delta^{15}N$	9	850.56	1.31	831.88	0.07
		land	7	850.87	1.62	836.44	0.06
		land + sex + $\delta^{13}C$	9	851.27	2.03	832.58	0.05
		land + sex + $\delta^{13}C$	9	851.27	2.03	832.58	0.05
		land + sex + $\delta^{15}N$ + land × sex	10	851.28	2.04	830.44	0.05
		sex	7	851.32	2.08	836.9	0.05
		land + sex + $\delta^{15}N$ + land × $\delta^{15}N$	10	851.56	2.31	830.72	0.04
		land + sex + $\delta^{15}N$ + $\delta^{15}N$ × sex	10	851.71	2.47	830.88	0.04
		land + sex + $\delta^{13}C$ + land × sex	10	852.01	2.76	831.16	0.03
		land + $\delta^{15}N$	8	852.45	3.20	835.9	0.03
		sex + $\delta^{15}N$	8	852.68	3.44	836.14	0.02

land + sex + $\delta^{13}C$ + $\delta^{15}N$	10	852.69	3.44	831.84	0.02
null	6	853.03	3.79	840.72	0.02
sex + $\delta^{13}C$	8	853.21	3.96	836.66	0.02
land + sex + $\delta^{13}C$ + land × $\delta^{13}C$	10	853.33	4.09	832.5	0.02
land + sex+ $\delta^{13}C$ + $\delta^{13}C$ × sex	10	853.43	4.18	832.58	0.02
land + sex + $\delta^{13}C$ + $\delta^{15}N$ + land × sex	11	853.44	4.20	830.44	0.02
land + $\delta^{15}N$ + land × $\delta^{15}N$	9	853.48	4.24	834.8	0.02
land + sex + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{15}N$	11	853.73	4.48	830.72	0.01
land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{15}N$ × sex	11	853.85	4.61	830.84	0.01
sex + $\delta^{15}N$ + $\delta^{15}N$ × sex	9	853.88	4.63	835.2	0.01
land + $\delta^{13}C$ + $\delta^{15}N$	9	854.59	5.34	835.9	0.01
sex + $\delta^{13}C$ + $\delta^{15}N$	9	854.64	5.39	835.96	0.01
$\delta^{15}N$	7	854.69	5.45	840.28	0.01
land + sex + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{13}C$	11	854.8	5.56	831.78	0.01
land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$	11	854.84	5.60	831.84	0.01
land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × sex	11	854.86	5.61	831.84	0.01
$\delta^{13}C$	7	855.06	5.81	840.64	0.01
land + $\delta^{13}C$ + land × $\delta^{13}C$	9	855.06	5.82	836.38	0.01
sex + $\delta^{13}C$ + $\delta^{13}C$ × sex	9	855.34	6.10	836.66	0.01
land + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{15}N$	10	855.6	6.36	834.76	0.01

	land + sex+ $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$ + land × sex	12	855.63	6.38	830.42	0.01
PC 1	sex	7	862.69	0.00	848.28	0.17
	land + sex	8	862.96	0.27	846.42	0.33
	sex + $\delta^{15}N$	8	864.67	1.97	848.12	0.07
	land + sex + land × sex	9	864.69	1.99	846.00	0.06
	sex + $\delta^{13}C$	8	864.72	2.03	848.18	0.07
	land + sex + $\delta^{15}N$	9	864.96	2.27	846.28	0.06
	land + sex + $\delta^{13}C$	9	865.08	2.38	846.40	0.06
	sex + $\delta^{15}N$ + $\delta^{15}N$ × sex	9	866.53	3.84	847.84	0.03
	land + sex + $\delta^{15}N$ + land × sex	10	866.70	4.01	845.86	0.02
	land + sex + $\delta^{15}N$ + land × $\delta^{15}N$	10	866.75	4.05	845.90	0.02
	sex + $\delta^{13}C$ + $\delta^{15}N$	9	866.75	4.06	848.08	0.02
	sex + $\delta^{13}C$ + $\delta^{13}C$ × sex	9	866.81	4.11	848.12	0.02
	land + sex + $\delta^{13}C$ + land × sex	10	866.81	4.11	845.96	0.02
	land + sex + $\delta^{15}N$ + $\delta^{15}N$ × sex	10	866.85	4.15	846.00	0.02
	land + sex + $\delta^{13}C$ + land × $\delta^{13}C$	10	867.03	4.34	846.20	0.02
	land + sex + $\delta^{13}C$ + $\delta^{15}N$	10	867.12	4.42	846.28	0.02
	land + sex + $\delta^{13}C$ + $\delta^{13}C$ × sex	10	867.18	4.48	846.34	0.02
	sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$	10	868.19	5.50	847.36	0.01

	sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{15}N$ × sex	10	868.62	5.92	847.78	0.01
	land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$	11	868.73	6.03	845.72	0.01
	sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × sex	10	868.85	6.16	848.02	0.01
	land + sex + $\delta^{13}C$ + $\delta^{15}N$ + land × sex	11	868.87	6.17	845.86	0.01
	land + sex + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{15}N$	11	868.92	6.22	845.90	0.01
	land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{15}N$ × sex	11	869.01	6.32	846.00	0.01
	land + sex + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{13}C$	11	869.08	6.38	846.06	0.01
	land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × sex	11	869.23	6.54	846.22	0.01
	null	6	969.09	106.39	956.78	0.00
BCI	land + sex	8	837.26	0.00	820.72	0.17
	land + sex + land × sex	9	837.61	0.36	818.92	0.14
	land + sex + $\delta^{15}N$	9	838.69	1.44	820.02	0.08
	land + sex + $\delta^{15}N$ + land × sex	10	839.11	1.85	818.28	0.07
	sex	7	839.22	1.97	824.80	0.06
	land + sex + $\delta^{13}C$	9	839.38	2.12	820.70	0.06
	land + sex + $\delta^{15}N$ + land × $\delta^{15}N$	10	839.66	2.40	818.82	0.05
	land + sex + $\delta^{13}C$ + land × sex	10	839.76	2.51	818.92	0.05
	land + sex + $\delta^{15}N$ + $\delta^{15}N$ × sex	10	839.93	2.67	819.08	0.04
	sex + $\delta^{15}N$	8	840.71	3.46	824.16	0.03

		land + sex + $\delta^{13}C$ + $\delta^{15}N$	10	840.85	3.59	820.00	0.03
		land + sex + $\delta^{13}C$ + $\delta^{15}N$ + land × sex	11	841.27	4.02	818.26	0.02
		sex + $\delta^{13}C$	8	841.28	4.02	824.74	0.02
		land + sex + $\delta^{13}C$ + land × $\delta^{13}C$	10	841.39	4.13	820.54	0.02
		land + sex + $\delta^{13}C$ + $\delta^{13}C$ × sex	10	841.53	4.27	820.68	0.02
		land + sex + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{15}N$	11	841.78	4.52	818.76	0.02
		sex + $\delta^{15}N$ + $\delta^{15}N$ × sex	9	841.99	4.73	823.30	0.02
		land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{15}N$ × sex	11	842.10	4.84	819.08	0.01
		sex + $\delta^{13}C$ + $\delta^{15}N$	9	842.81	5.55	824.12	0.01
		land + sex + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{13}C$	11	842.91	5.66	819.90	0.01
		land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$	11	842.98	5.73	819.98	0.01
		land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × sex	11	843.02	5.76	820.00	0.01
		sex + $\delta^{13}C$ + $\delta^{13}C$ × sex	9	843.41	6.15	824.72	0.01
		land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$ + land × sex	12	843.44	6.19	818.24	0.01
		land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$ + land × $\delta^{15}N$	12	843.96	6.70	818.76	0.01
		sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{15}N$ × sex	10	844.10	6.84	823.26	0.01
		land + sex + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$ + $\delta^{15}N$ × sex	12	844.26	7.00	819.06	0.01
		null	6	849.53	12.27	837.20	0.00
Nestlings	Mass	land	8	544.07	0.00	527.00	0.22

	null	7	544.20	0.13	529.38	0.20
	$\delta^{13}C$	8	545.74	1.68	528.68	0.09
	land + $\delta^{15}N$	9	545.78	1.71	526.44	0.09
	land + $\delta^{13}C$	9	546.34	2.27	527.00	0.07
	$\delta^{15}N$	8	546.42	2.36	529.36	0.07
	land +$\delta^{15}N$ + land × $\delta^{15}N$	10	547.11	3.04	525.46	0.05
	land + $\delta^{13}C$ + land × $\delta^{13}C$	10	547.12	3.05	525.48	0.05
	land + $\delta^{13}C$ + $\delta^{15}N$	10	547.98	3.91	526.34	0.03
	$\delta^{13}C$ + $\delta^{15}N$	9	548.01	3.94	528.68	0.03
	land + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{13}C$	11	548.69	4.63	524.70	0.02
	land + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{15}N$	11	548.72	4.65	524.74	0.02
	land + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{13}C$ + land × $\delta^{15}N$	12	549.17	5.10	522.80	0.02
	$\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$	10	550.02	5.96	528.38	0.01
	land + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$ + land × $\delta^{15}N$	12	550.06	5.99	523.70	0.01
	land + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$	11	550.22	6.16	526.24	0.01
	land + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$ + land × $\delta^{13}C$	12	550.98	6.91	524.62	0.01
PC1	null	7	489.43	0.00	474.62	0.29
	land	8	490.05	0.62	473.00	0.21
	$\delta^{13}C$	8	491.52	2.09	474.46	0.10

	δ^{15}N	8	491.66	2.23	474.60	0.10
	land + δ^{13}C	9	492.28	2.85	472.94	0.07
	land + δ^{15}N	9	492.31	2.89	472.98	0.07
	δ^{13}C + δ^{15}N	9	493.79	4.36	474.46	0.03
	land +δ^{15}N + land × δ^{15}N	10	494.02	4.59	472.38	0.03
	land + δ^{13}C + land × δ^{13}C	10	494.57	5.14	472.92	0.02
	land + δ^{13}C + δ^{15}N	10	494.58	5.15	472.94	0.02
	δ^{13}C + δ^{15}N + δ^{13}C × δ^{15}N	10	495.29	5.86	473.66	0.02
	land + δ^{13}C +δ^{15}N + δ^{13}C ×δ^{15}N	11	496.10	6.67	472.12	0.01
	land + δ^{13}C +δ^{15}N + land × δ^{15}N	11	496.36	6.93	472.38	0.01
	land + δ^{13}C +δ^{15}N + land × δ^{13}C	11	496.91	7.48	472.92	0.01
BCI	land	8	519.86	0.00	502.80	0.21
	land + δ^{13}C	9	521.15	1.29	501.82	0.11
	null	7	521.18	1.32	506.36	0.11
	land + δ^{13}C + land × δ^{13}C	10	521.25	1.39	499.62	0.10
	land +δ^{15}N	9	521.34	1.48	502.00	0.10
	land + δ^{13}C + δ^{15}N	10	522.24	2.38	500.60	0.06
	land + δ^{13}C +δ^{15}N + land × δ^{13}C	11	522.64	2.77	498.66	0.05
	land +δ^{15}N + land × δ^{15}N	10	523.07	3.21	501.42	0.04

land + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{15}N$	11	523.27	3.40	499.28	0.04
$\delta^{13}C$	8	523.37	3.50	506.30	0.04
$\delta^{15}N$	8	523.41	3.55	506.34	0.04
land + $\delta^{13}C$ + $\delta^{15}N$ + land × $\delta^{13}C$ + land × $\delta^{15}N$	12	523.43	3.57	497.06	0.04
land + $\delta^{13}C$ +$\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$	11	524.50	4.63	500.52	0.02
land + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$ + land × $\delta^{13}C$	12	524.99	5.13	498.62	0.02
land + $\delta^{13}C$ + $\delta^{15}N$ + $\delta^{13}C$ × $\delta^{15}N$ + land × $\delta^{15}N$	12	525.49	5.63	499.12	0.01
$\delta^{13}C$ + $\delta^{15}N$	9	525.63	5.77	506.30	0.01

[1] Number of estimable parameters.

[2] Akaike's Information Criterion, corrected for small sample sizes.

[3] Difference in AIC_c between each model and the model with the lowest AIC_c value.

[4] -2 × Log Likelihood.

[5] Model weight.